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THE CRANIAL MORPHOLOGY OF THE LOWER LIASSIC LATIPINNATE ICHTHYOSAURS OF ENGLAND

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C. McGOWAN

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BY

CHRISTOPHER McGOWAN

Royal Ontario Museum, Toronto

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THE CRANIAL MORPHOLOGY OF THE LOWER LIASSIC LATIPINNATE ICHTHYOSAURS OF ENGLAND

By C. McGOWAN

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SYNOPSIS

An account of the anatomy of the ichthyosaurian skull is given based upon several prepared and part-prepared specimens. It is shown that the temporal vacuity is bounded by the squamosal, postfrontal and parietal, the supratemporal being absent. As a result the Ichthyosauria can be removed from their phyletic isolation and placed with the plesiosaurs in the Subclass Euryapsida.

An attempt is made to reconstruct certain aspects of the soft anatomy including the membranous labyrinth, brain, and jaw musculature and the light this casts upon the ichthyosaurian way of life is examined. A detailed account of the individual elements of the skull is given.

INTRODUCTION

In 1814 the discovery of a new group of fossil animals was heralded by Sir Everard Home with the publication of, 'Some account of the fossil remains of an animal more nearly allied to fishes than to any other classes of animals'. This paper figured and described a large skull[1] which had been collected on the beach at Lyme Regis, and is the first account of the cranial morphology of an ichthyosaur. There have been many other accounts of the cranial morphology since 1814, including two very detailed papers on *Ophthalmosaurus* (Andrews, 1910), and on *Ichthyosaurus* (Sollas, 1916), but even here there were shortcomings. Whereas the structure of the palate, lower jaw, and much of the dermal skull roof had been satisfactorily interpreted, there had been much confusion in the temporal and occipital regions, and the problem of the otic capsule remained largely unresolved. Furthermore, little progress was made in the reconstruction of the soft anatomy, and there have been inadequacies in the descriptions of individual cranial elements.

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[1] This skull is now in the British Museum (Nat. Hist.) and an extensive search into the literature and the records of the Museum has revealed a weight of evidence to support the conclusion that this was Mary Anning's first ichthyosaur.

Most of the information in this present study has been obtained from material extracted from nodules by acetic acid, and the fine state of preservation has permitted an accurate reconstruction of the hind portion of the skull to be made. The successful interpretation of the skull has had a far reaching effect, for it clearly demonstrates the absence of a supratemporal, the temporal vacuity being in fact bounded by the squamosal, postfrontal and parietal. In consequence the Ichthyosauria can be removed from their phyletic isolation and placed with the plesiosaurs and protorosaurs in the subclass Euryapsida. An attempt has been made to reconstruct certain aspects of the soft anatomy which gives some insight into the ichthyosaurian way of life. For the sake of completeness a detailed description of the individual cranial elements is given, but before turning to the morphological account a brief history of research on the cranial morphology will be outlined.

HISTORY OF CRANIAL RESEARCH

The first account of the ichthyosaurian skull was given by Sir Everard Home in 1814 in a paper which was also the first notification of the discovery of the new group of animals. Home was largely preoccupied with unravelling the problem of the affinities of this new find, although he did take note of certain cranial features. He observed that tooth replacement occurred, and compared it with the crocodilian condition, and noted the apparent presence of a retroarticular process. There was some confusion in the position of the external narial aperture, largely because it was partly occluded by a displaced sclerotic plate, and its true position was not established. Home published several more papers during the next few years, and in 1820 a paper appeared in which a second skull was figured (probably of *I. breviceps*), together with a section through the snout and lower jaw.

By 1821 a sufficient amount of cranial material had accumulated to permit a more exhaustive treatment, and in that year Conybeare published a joint paper with De la Beche dealing largely with the skull. The confusion in the position of the external naris was removed, and, notwithstanding certain anomalies in the terminology used, a very good account of the lower jaw was given, accompanied by a number of excellent figures including several transverse sections. The entire dorsal surface of the skull was figured, although some errors were made. The parietal and frontal were both described as unpaired elements, and it was believed that the prefontal, postfrontal, and postorbital were not separate elements but processes of the frontal. It is interesting to note that only one element was shown in the temporal region, and this was described as, 'portions of the temporal bones'. The account of the palate was very much confused, and, in the absence of the hind skull, no account of the occiput could be given. Five years later, in 1824, Conybeare published a further account in which he discussed how, 'Mr De la Beche long since believed himself able, from the examination of the teeth, combined with some other characters, to establish three species, to which he has applied the names *communis*, *platyodon* and *tenuirostris*: and to these our joint observations have recently added a fourth, *Ichthyosaurus intermedius*.' A number of teeth are figured and described, and the structure of the lower jaw is further discussed. Additional transverse sections through the jaw are given and the prearticular is figured for the first time (referred to as the 'crescent-shaped bone'). The temporal vacuity is discussed in further detail and compared with the upper temporal vacuity of the crocodile. Once more the paucity of occipital material prevented adequate account of the hind skull, but an admittedly conjectural reconstruction of the occiput was given, based upon a number of incomplete specimens.

Owen's Report to the British Association for 1839 includes an account of the cranial morphology of ichthyosaurs, but in the absence of figures and in the use of a confusing osteological nomenclature, his account is difficult to follow. The occipital region is discussed and although he recognized that the supraoccipital participated in the formation of the foramen magnum (Owen 1839 : 90), he refers on the next page to an element which, from its description, can only be the supraoccipital, but which is referred to as the interparietal. The basioccipital condyle is described but it is considered that the exoccipitals contribute to the articulation with the axial skeleton. The palate is described, but the true position of the internal narial aperture is not established, being confused with the interpterygoid vacuity. Owen discusses the robust nature of the quadrate and its firm bracing against the rest of the skull with reference to the powerful adduction of the lower jaw.

In 1880 Seeley figured and described the skull of a new species, *I. zetlandicus*. Of significance is the fact that the margin of the temporal vacuity is correctly shown to be formed by the parietal, postfrontal, and squamosal, but a second temporal element is shown lying between the squamosal and quadratojugal, and referred to as the supraquadrate.

Many excellent figures of skulls are included in Owen's (1881) Monograph on the Liassic Reptilia, accompanied by detailed descriptions. The problem of the palate is largely resolved, although the pterygoid is shown to overlap the palatine (Owen's ectopterygoid) dorsally, and the position of the internal naris is correctly established (Owen 1881 : plate 25). A good attempt is made to reconstruct the occiput (Owen 1881 : plate 24, fig. 1), and his previous error concerning the participation of the exoccipital in the articular condyle is corrected. The supraoccipital is correctly figured wedged in the notch formed by the two parietals, while the opisthotic (Owen's paroccipital) is shown as a strut between the basioccipital medially and the quadrate distally, although from Owen's figure it would seem that this element is in fact the stapes. It is recorded that the anterior portion of the basioccipital is notched or grooved in some species, 'as if for the outlet of the Eustachian canal.' The quadrate (tympanic) is shown in its correct relationship with the rest of the skull, and the foramen which it forms with the quadratojugal (zygomatic) is described as the auditory meatus. Referring to the neurocranium Owen writes, 'the side walls of the brain case proper seem to have been mainly cartilaginous.' A satisfactory description of the skull roof is given (Owen 1881 : 96, pl. 23, fig. 1), and in the temporal region the posterior and posterolateral margin of the vacuity is shown to be formed by the large triradiate squamosal (mastoid). A second temporal element, however, is figured lying immediately beneath the squamosal, referred to as the prosquamosal, and beneath this is an element described as the zygomatic, (quadratojugal).

Fraas (1891) figures a number of skulls, both unprepared and prepared, and also some excellent sections through teeth. A lateral view of a skull of *I. zetlandicus* is given (Fraas 1891 : pl. 2, fig. 1), in which there is a satisfactory relationship between the individual elements, but here again a second element is figured lying between the squamosal dorsally and the quadratojugal ventrally. The misconception that there were two elements in the temporal region was by this time firmly established in the literature. In a reconstruction of the occiput of a specimen of *I. quadriscissus* the opisthothic is shown on the same horizontal level as the exoccipital, the proötic is oriented between the opisthotic and stapes, and the supraoccipital is shown lying outside the parietals. It is interesting to note that neither the opisthotic or the stapes are shown to have distal contact with the rest of the skull, and the present investigation has shown that there was almost certainly a cartilaginous intervention in both cases. An oblique view of the hind skull of a British Museum (Natural History) specimen from Lyme Regis is quite satisfactory but for the inversion of the epipterygoids. A number of individual elements are figured.

A very thorough description of the skull and post-cranial skeleton of *Ophthalmosaurus* was given in 1910 by C. W. Andrews. The individual skull elements are figured and described in detail, although their relationships are not always completely known. The squamosal is correctly shown to form the posterior and postero-lateral margin of the temporal vacuity, but in a restoration of the entire skull (Andrews 1910 : fig. 23), a second temporal element, the supratemporal, is shown immediately beneath it. The supratemporal is not figured as an individual element since it is said to have been missing or crushed beyond recognition in most cases, but reference is made to one specimen (R2740) in which this element can apparently be seen as a roughly triangular bone. The impressions of the membranous labyrinth in the proötic and opisthotic are described, but, since it was realised that the proötic did not have osseous contact with the rest of the skull, it was not oriented. In the lower jaw the articular is shown in its correct relationship with the other elements (Andrews 1910 : fig. 20a), and its facet for reception of the prearticular (described as the coronoid) is clearly demonstrated. A very satisfactory reconstruction of the occipital region is given.

In a discussion of the homologies of the bones in the temporal region in reptiles Watson (1914) concluded that the 'inner bone' of the temporal region in *Ichthyosaurus*, described by Andrews in *Ophthalmosaurus* as the supratemporal, was really the squamosal, but he went on to conclude that, 'this view has the great disadvantage of leaving unexplained the outer temporal element.'

The most extensive and informative cranial investigation was that of Sollas (1916), based on the study of serial sections. The squamosal is figured and described in its true light, but, although no supratemporal was present in the material sectioned, Sollas preferred to conclude that, 'This bone, as is commonly the case with *Ichthyosaurus* skulls, is missing.' The opisthotic was interpreted as resting with its paroccipital process in contact with the quadrate and pterygoid, while the proötic was not oriented. The great value of this excellent study lies in the fact that the precise relationships existing between individual elements at the time of preservation can be determined, but it suffers from the unavoidable shortcoming that the individual elements could not be adequately figured and described.

Von Huene's monograph (1922) on the Liassis ichthyosaurs includes a number of figures of skulls and of some isolated elements, but little detail is given. Two elements are figured in the temporal region; that bordering the temporal vacuity is described as the supratemporal, the one below as the squamosal. Later, in 1949, von Huene figured the back of a skull of *P. acutirostris* showing a good relationship between the stapes, exoccipital and opisthotic, but the proötic is shown lying dorsolateral to the exoccipital, and the basioccipital is inverted. An interparietal is figured, and, once again, two elements are shown in the temporal region.

Appleby (1956) in a paper on the osteology of *Ophthalmosaurus* describes the bone which forms the postero-lateral margin of the temporal vacuity as the supratemporal, and writes that, 'Between the bone in question (the supratemporal) and the quadrate on the external surface is a thin plate of bone which is rarely seen in *Ophthalmosaurus* but which meets the jugal, quadratojugal and postorbital and is therefore the true squamosal.' In a more recent paper Appleby (1961) gives an account of the cranial morphology of ichthyosaurs, and, as will be shown later, his interpretation of the otic region is at variance with the conclusions which have been drawn in the present investigation.

In the winter of this year Romer (1968) published a paper on, 'An ichthyosaur skull from the Cretaceous of Wyoming,' in which the whole problem of the supratemporal and squamosal is looked into. Romer reaches the same conclusions as the present author, and includes some fine figures of material which D. M. S. Watson had worked upon.

CRANIAL MATERIAL EXAMINED DURING THE INVESTIGATION

Six prepared or partly prepared skulls were examined, together with some sixty compressed specimens.

A brief description of the six specimens, together with the state of their preservation, is given in Table 1.

TABLE 1

Museum No.	Description	State of Preservation
R8177	A moderately large partial skull not complete beyond the nares. The individual elements have been completely extracted from the matrix.	Most of the extracted elements are in a fine state of preservation and includes the palatal elements. Not all elements are present.
R6697	A small specimen similar to R8177 but far less complete.	Only part of the pterygoid is present and many of the elements of the left side are missing. Skull roof represented only by incomplete parietals.

TABLE I (*continued*)

Museum No.	Description	State of Preservation
Evans' nodule	Similar to specimen R6697 but includes the anterior portion of the axial skeleton.	The majority of the elements present are in a fine state of preservation.
R1168	A partial skull similar in size to R6697. The individual elements have been, in part, extracted from the matrix.	The preservation of the bone is poor and the presence of veins of insoluble substances in the matrix made preparation difficult.
R3375	A moderately large and near complete skull, dorso-ventrally compressed, lying embedded in a relatively soft and shaley matrix.	The dorsal surface is exposed, the ventral portion is hidden from view and much crushed.
49203	An in-the-round specimen similar in size to R3375. The lower jaw has been removed.	The bone is not as well preserved as in the ex-nodular material.

With the exception of specimen 49203 the six prepared skulls were in a condition which prevented identification to species level. However, from the evidence available, it would seem that all six were latipinnate, and therefore to be assigned to the genus *Ichthyosaurus.* Specimen 49203 could be referred to the species *I. communis.* [The systematics of the Lower Liassic ichthyosaurs are discussed in detail by the present author in a paper which is now in preparation.]

DESCRIPTION OF INDIVIDUAL ELEMENTS OF THE SKULL

With the exception of the nasal, maxilla and premaxilla the elements of the skull were complete and well preserved in the material examined. In the case of these three elements references to unprepared skulls and serial sections has contributed to their descriptions. The descriptions will be given in two main sections, the replacement bones, and the dermal bones.

REPLACEMENT BONES

A. *Ossifications of the chondrocranium*

The ossified chondrocranium is represented by six elements, the basisphenoid, basioccipital, supraoccipital and paired exoccipitals, opisthotics and proötics. The opisthotic and proötic together form the greater part of the ossified otic capsule, with a minor contribution from the supraoccipital.

1. *Basisphenoid* (fig. 1, plate 1a). The basisphenoid is a fairly stout dorso-ventrally compressed element which contributes to the floor of the cranium. Posteriorly it articulates with the basioccipital, and on either side ventro-laterally with the pterygoids.

The posterior surface faces obliquely backwards and upwards and is indented to receive the keeled anterior face of the basioccipital. This indentation continues rostrally as a fairly deep and narrow ascending fissure which bisects the dorsal surface. Anteriorly the dorsal edges of the fissure are raised into a pair of pinnacles, and in one mature specimen (R8177) these processes have fused in the mid-line forming a bony buttress. It is thought that the fissure probably marks the position of a vestige of the upturned tip of the notochord, and this matter is referred to again when the reconstruction of the occiput is discussed (page 76).

Ventrally, on each side, the basisphenoid is drawn out into the winged basipterygoid process which slots into a corresponding depression in the pterygoid. The bone which borders the dorsal edge of the basipterygoid process has a spinous rugosity and in mature individuals the spines are quite prominent. The element is pierced by a wide channel which follows an oblique path, entering on the anterior face, and leaving from the posterior half of the ventral face. This channel, the carotid foramen, served to carry the two internal branches of the carotid artery to the brain.

The carotid foramen widens as it opens into the endocranial cavity, forming a rounded depression which is interpreted as the sella turcica. In life the sella turcica housed the pituitary gland and the bony arch above it, which is notched by the dorsal fissure (see fig. 1a) represents the ossified dorsum sellae. Immediately below the sella turcica is a pair of rounded depressions which are immediately underlain by the dermal parasphenoid. Similar paired depressions are found in the basisphenoid of *Sphenodon* where they have been interpreted as impressions of the paired trabeculae in the anterior portion of the ossified parachordal basal plate,

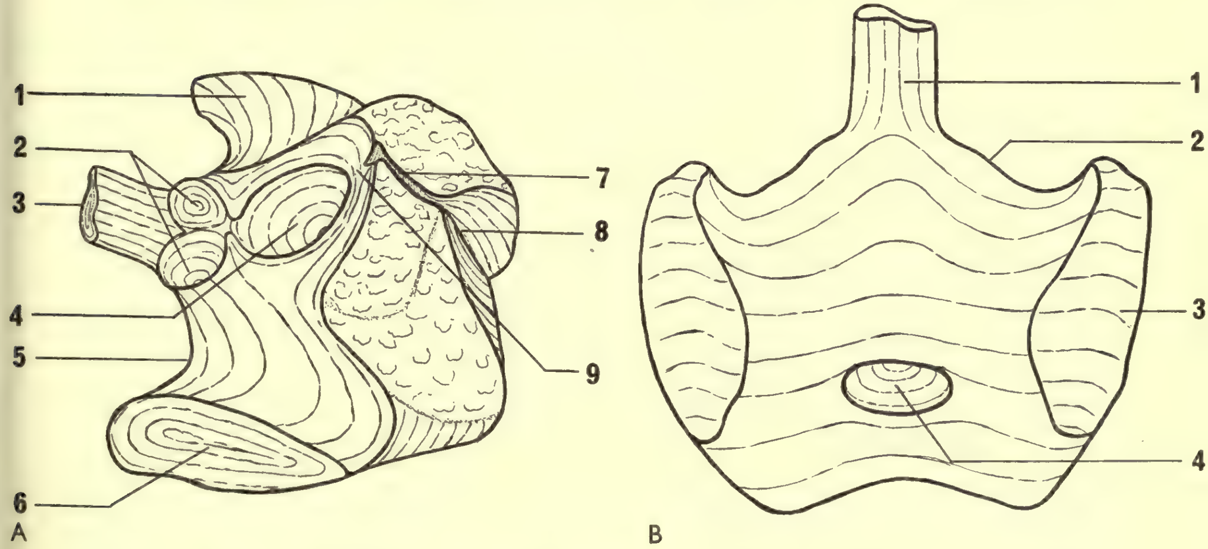


FIG. 1. (a). Basisphenoid, dorso-lateral view, ×2, (Evans' nodule). 1, Basipterygoid process. 2, impressions of paired trabeculae. 3, parasphenoid. 4, sella turcica. 5, leading ventral edge which contributes to the interpterygoid vacuity. 6, distal articular facet of basipterygoid process. 7, dorsal fissure. 8, keeled posterior surface. 9, ossified dorsum sellae. (b). Basisphenoid, ventral view, ×2, (Evans' nodule). 1, parasphenoid. 2, leading ventral edge. 3, ventral articular facet of basipterygoid process. 4, ventral opening of carotid foramen.

(Säve-Söderberg 1946). On either side of these depressions the leading ventral edge of the basisphenoid is emarginated, and is continuous with the curvature of the interpterygoid vacuity.

To the ventral surface of the basisphenoid is applied the dermal parasphenoid, and their relationship is so intimate that the actual extent of the latter is difficult, if not impossible, to determine. Sufficient remains of the parasphenoid to indicate that it was elevated at about 60 degrees to the horizontal.

2. *Basioccipital* (fig. 2, plate 1b). The basioccipital, the most posterior of the cranial series, is a stout and compact bone which bears the condyle for articulation with the vertebral column. Anteriorly and ventrally it articulates with the basisphenoid, dorsally with the exoccipitals. Postero-laterally it articulates with the opisthotic, and a little below this it makes touch contact with the proximal head of the stapes.

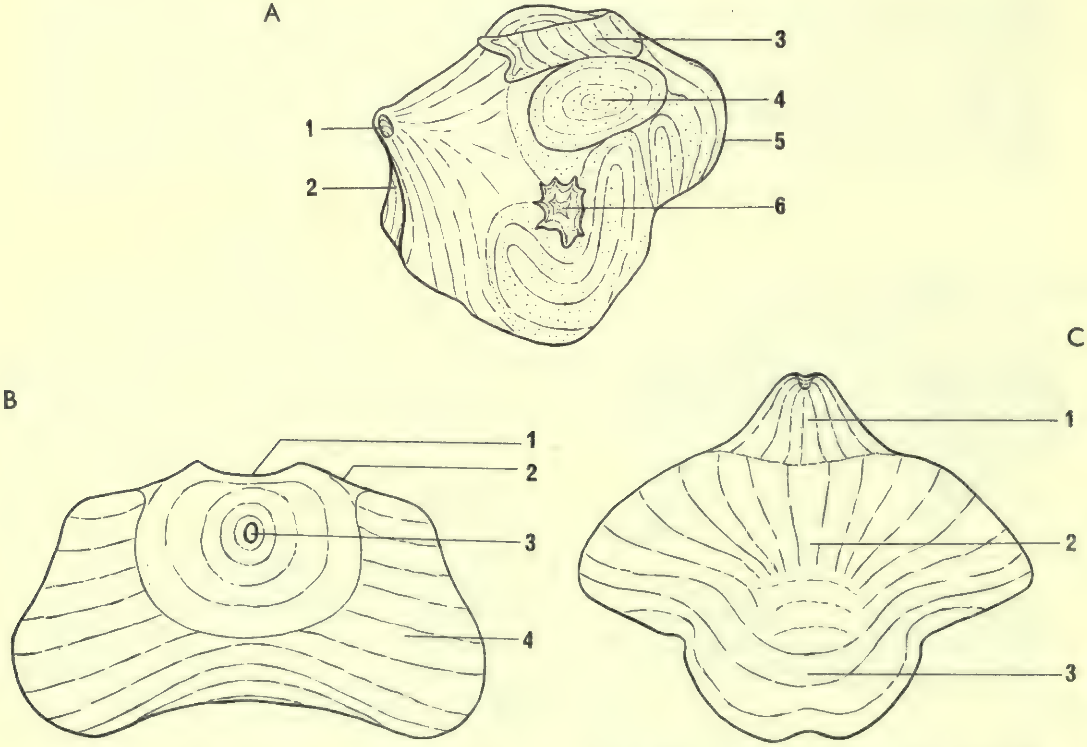


FIG. 2. (a). Basioccipital, antero-lateral view, $\times\frac{3}{2}$ (Evans' nodule). 1, notched tip of basioccipital peg. 2, keeled antero-ventral face. 3, floor of neurocranium. 4, exoccipital facet. 5, condyle. 6, stellate excavation probably marking position of lagena. (b). Basioccipital, posterior view, $\times\frac{3}{2}$ (Evans' nodule). 1, floor of foramen magnum. 2, exoccipital facet. 3, depression at centre of condyle. 4, posterior shield. (c). Basioccipital, ventral view, $\times\frac{3}{2}$ (Evans' nodule). 1, basioccipital peg. 2, ventral surface. 3, condyle.

The condyle is a spherical outpushing from the dorsal half of the posterior surface, and bears a small depression at its centre which has been interpreted by Andrews in *Ophthalmosaurus* (1910 : 6) as marking the position of the anteriormost remnant of the notochord. Since it is thought that the dorsal fissure in the basisphenoid marks the position of a vestige of the upturned notochordal tip, the depression in the condyle cannot represent the anterior most tip of the notochord. The true situation would seem to be that at least two vestiges of the notochord persisted in the skull and that the depression in the condyle marks the anterior tip of the second of these. When viewed from behind the rounded outline of the condyle is interrupted dorsally by the floor of the foramen magnum. Laterally and ventrally the posterior surface slopes away from the condyle, producing a curving shield of bone which continues, without interruption, with the ventral surface.

The dorsal surface is grooved in the midline by a shallow but wide excavation which bifurcates anteriorly into two tapering tongues, and which forms the floor of the cranial cavity. On either side is a large ovoid facet for the reception of the exoccipital. The dorsal surface is not horizontal, but slopes forward, and, just anterior to the median groove the slope becomes steeper. In addition to shelving, the dorsal surface is tapered, and because the lateral and ventral surfaces are similarly tapered, the bone is drawn out to a point, and this tapering process will be referred to as the basioccipital peg.

The ventral surface is of two parts; a posterior portion slopes upwards to become continuous with the posterior shield, and an anterior portion slopes upwards to become continuous with the basioccipital peg. In mid-ventral line the anterior portion is raised by a ridge and the keel thus formed corresponds closely with the postero-dorsal surface of the basisphenoid which is sculptured for its reception. Just beneath the tip of the basioccipital peg there is a small notch, and when the basioccipital and basisphenoid are placed in contact it is seen to align with the dorsal fissure in the basisphenoid. This notch is interpreted as marking the posterior end of the anterior notochordal vestige, a conclusion supported by the fact that the width of the dorsal fissure in the basisphenoid compares very closely with that of the notch in the peg, which in turn compares with the notch in the condyle. This matter is discussed in some detail in a later section (see page 76).

Sloping away from the tip of the basioccipital peg, on either side, is an antero-lateral surface, and this bears a stellate excavation at its centre which is thought to mark the position of the lagena.

3. *Exoccipital* (fig. 3, plate 1c). The vertically orientated exoccipital is a small element of some complexity which lies at the back of the skull on either side of the foramen magnum forming the postero-lateral wall of the neurocranium. Dorsally it articulates with the supraoccipital, whilst ventrally it rests in an oval depression on the dorsal surface of the basioccipital.

Essentially the exoccipital comprises a solid and ovoid base connected by a narrow waist to a somewhat swollen head. The entire dorsal surface is formed of a rounded articular surface for the supraoccipital and is relatively smooth, faces obliquely forward and upward, and is inclined to the longitudinal axis so that the posterior edge lies medial to the anterior edge. The ventral surface is pitted and ridged, and is oval in outline, tapering anteriorly.

The element is pierced by three foramina which can be clearly seen in lateral view. Of these the most posterior is the largest, and is rounded rather than oval, whilst that adjacent to it is distinctly ovoid. Both foramina slope slightly antero-dorsally as

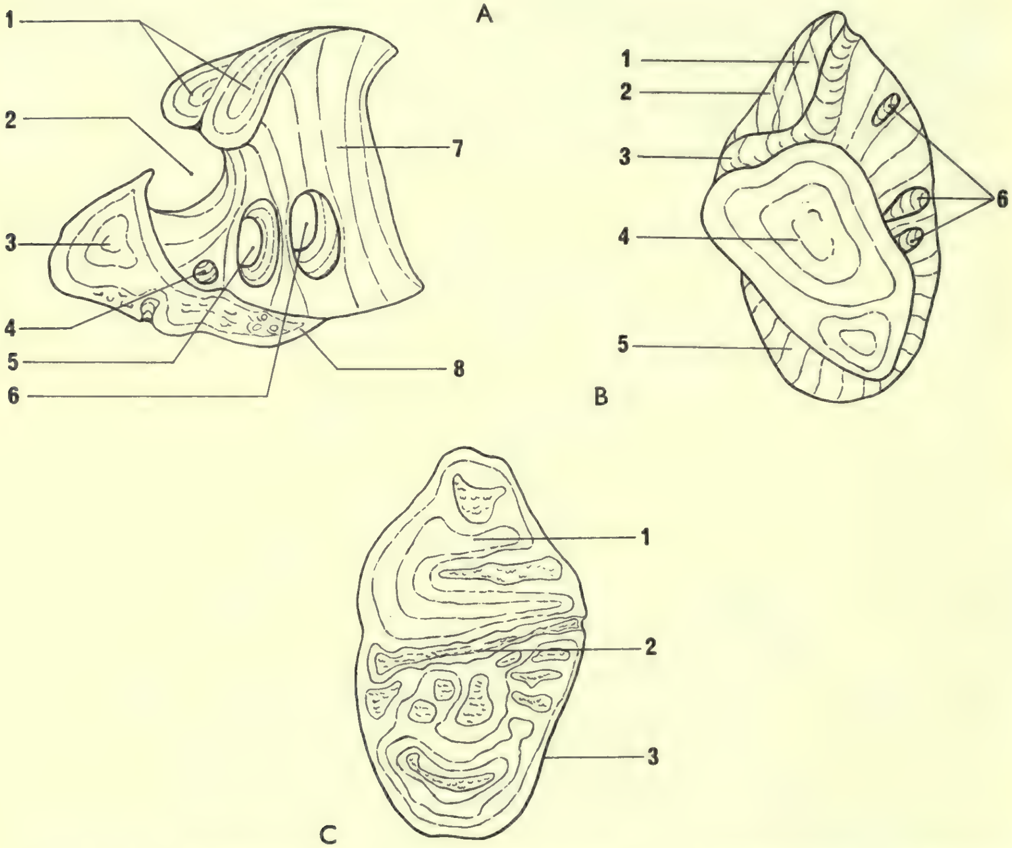


Fig. 3. (a). Exoccipital (left), external lateral view, ×3 (Evans' nodule). 1, supraoccipital facet. 2, jugular foramen. 3, triangular process. 4, anterior nervous foramen, possibly for transmission of the spinal accessory nerve. 5, nervous foramen for transmission of anterior branch of the hypoglossal nerve. 6, nervous foramen for transmission of posterior branch of hypoglossal nerve. 7, external lateral surface. 8, ventral basioccipital facet. (b). Exoccipital (left), dorsal view, ×3 (Evans' nodule). 1, medial edge of triangular process which was continuous with the cartilaginous wall of the otic capsule. 2, triangular process. 3, grooved floor of jugular foramen. 4, supraoccipital facet. 5, external lateral surface. 6, nervous foramina. (c). Exoccipital (left), ventral view, ×3 (Evans' nodule). 1, anterior portion of basioccipital facet. 2, transverse groove, probably marking the course of a blood vessel. 3, external lateral edge of basioccipital facet.

they pass outwards, and are slightly divergent. Anteriorly there is a prominent emargination, the jugular foramen, and just beneath it is the third and smallest foramen, which can easily be overlooked. As in the other foramina, it follows an antero-dorsal passage through the bone. The posterior aspect of the exoccipital has a curved profile in both external and internal view.

The jugular foramen served to transmit the jugular vein, the vagus nerve, and perhaps also the glossopharyngeal. The two large foramina are believed to have transmitted two branches of the hypoglossal, while the smallest may have carried the spinal accessory. The foramina will be discussed in greater detail below.

In front of the jugular foramen is a bony process which is triangular in external view and which has a relatively smooth face. This process is inclined both forward and outward, and is inflected anteriorly to form a narrow and medial bony lip which was continuous with the cartilaginous wall of the otic capsule. Anteriorly the internal surface of the bone is smooth, and follows a curved path which slopes backwards and upwards as it passes outward and is continuous with the floor of the jugular foramen. Posteriorly the internal surface is much interrupted by the passage of the nerve foramina.

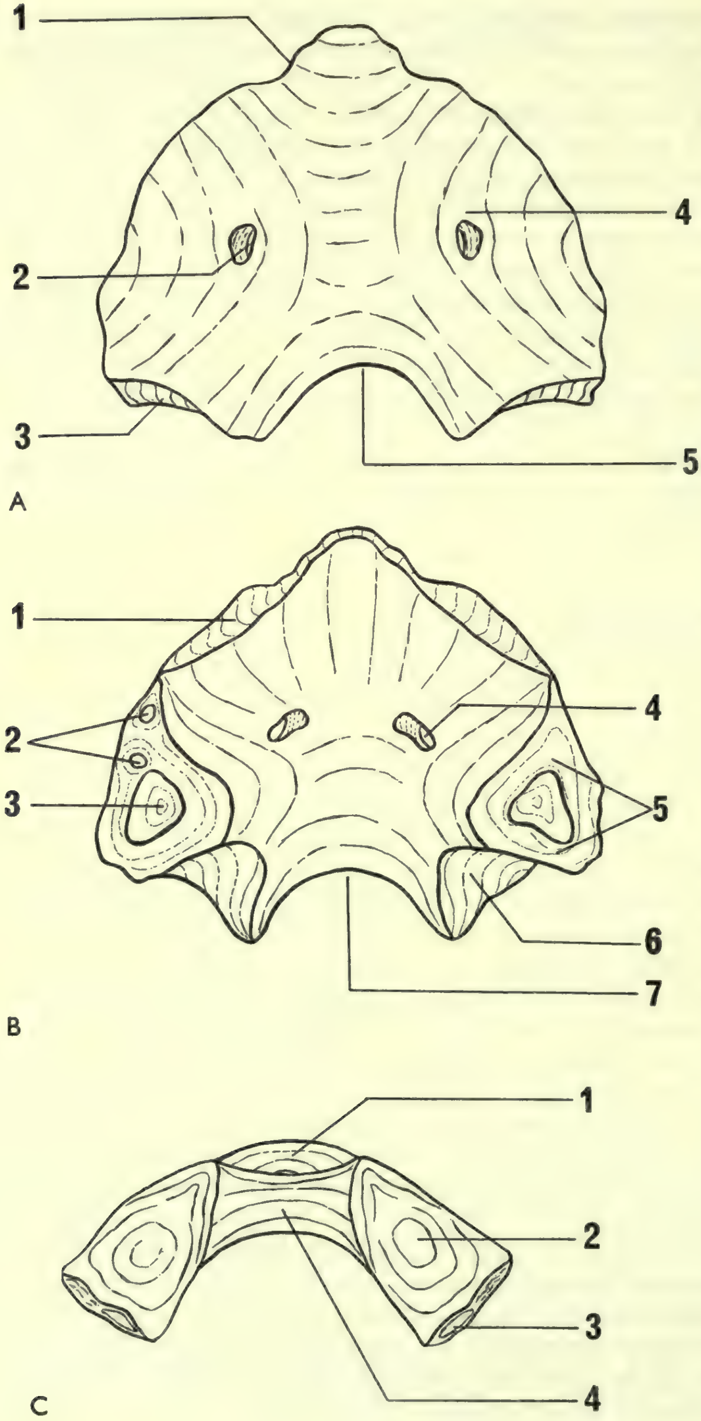
4. *Supraoccipital* (fig. 4, plate 1d). Resting on the paired exoccipitals the supraoccipital completes the occipital series, roofing the foramen magnum dorsally and forming the postero-dorsal wall of the neurocranium.

The posterior surface is convex from side to side and to a much lesser extent from top to bottom. The anterior surface is correspondingly concave from side to side giving it a strongly arched appearance when viewed from above. The bone is pierced by a pair of foramina which open out on the anterior and posterior surfaces of the bone. Due to divergence the foramina lie further apart on the posterior surface than they do anteriorly, and they are ovoid in shape rather than round. These openings may have served for the passage of the endolymphatic ducts, and the posterior surface of the supraoccipital is interrupted in the vicinity of each by a shallow triangular depression.

The dorsal edge is channeled by two shallow grooves on either side of the midline and also by a number of small depressions, and this marks the boundary between the ossified and cartilaginous portions of the neurocranium. Ventro-laterally the sculptured dorsal margin is continuous with the triangular lateral surface. This is also marked by small indentations which embrace a small and triangular depression of cancellar bone which bears an impression of the membranous labyrinth.

The exoccipital facets are petaloid when viewed from beneath, and occupy the entire ventral surface on either side of the foramen magnum. The facets are hollowed, and because the internal margin is more strongly arched than the external margin, the smooth articular surface is inclined slightly inwards.

The dorsal arch of the foramen magnum is variable, and does not necessarily have a perfect bilateral symmetry. In some specimens the arch is wide, as in Evans' nodule, and the foramen has a rounded outline, whereas in others a narrow arch confers a distinctly ovoid foramen, as in R6697.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5. *Opisthotic* (fig. 5, plate 1e). The opisthotic is a compact bone which lies at the back of the skull lodged between the basioccipital proximally, the squamosal distally, and has contact with the head of the stapes ventrally. Being the posterior (and major) ossification of the cartilaginous otic capsule, it bears impression of the membranous labyrinth on its anterior surface.

Viewed from behind the opisthotic has a triangular outline with its apex represented by the rounded paroccipital process, directed laterally and dorsally. The medial surface is largely occupied by a shallow and crescentic articular facet which faces obliquely to make contact with the periphery of the basioccipital.

The membranous impression represents the posterior aspect of the utriculus and sacculus and the origin of the horizontal semicircular canal, possibly also the origin of the posterior vertical semicircular canal. The horizontal semicircular canal impression branches off from a pear-shaped depression and follows a curving path which passes externally and slightly ventrally. The bone of the depressed area is marked by fine striations which follow the contours like the shading lines of a drawing. Circumscribing the impression is a margin of bone which is excavated by shallow grooves and pockets, having the same grooved and pitted appearance as the dorsal edge of the supraoccipital. In life this margin was continuous with the cartilaginous wall of the otic capsule, and gives a good indication of its thickness. Lying outside and just ventral of saccular impression is a second and very much smaller depression which is oval in shape and lined with cancellar bone similar in appearance to that of the membranous impression in the supraoccipital. This is interpreted as probably being the impression of part of the lagena.

6. *Proötic* (fig. 6, plate 1f). The proötic is the third and last of the otic elements and, lacking contact with any other element, is the most difficult to interpret. Only after the membranous labyrinth had been partly reconstructed was it possible to arrive at a satisfactory orientation, and it is within the framework of this new relationship that the element will now be described.

The proötic is a small bone which forms the anterior wall of the otic capsule, and its posterior aspect thus bears an impression of the membranous labyrinth. Since its walls are relatively thin it has become partially moulded to the shape of the labyrinth, and has the appearance of a pyramidal seashell whose umbo lies at its centre. The membranous impression is pear-shaped, with a wide branch coming off at right angles about half way down its external side, and represents the union of two semicircular canals. One of these, the narrower, lies in the vertical plane, and is interpreted as being that of the anterior vertical semicircular canal. The

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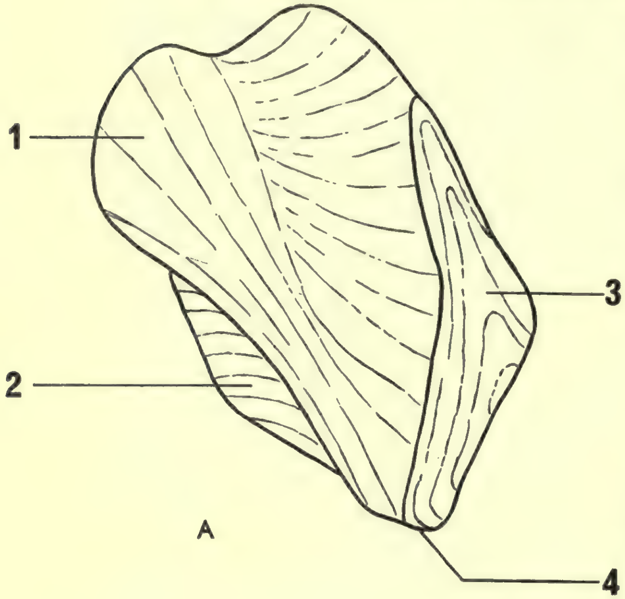
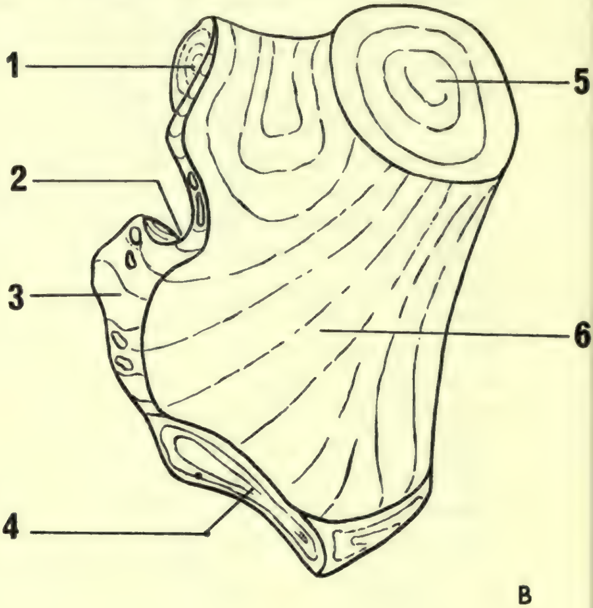
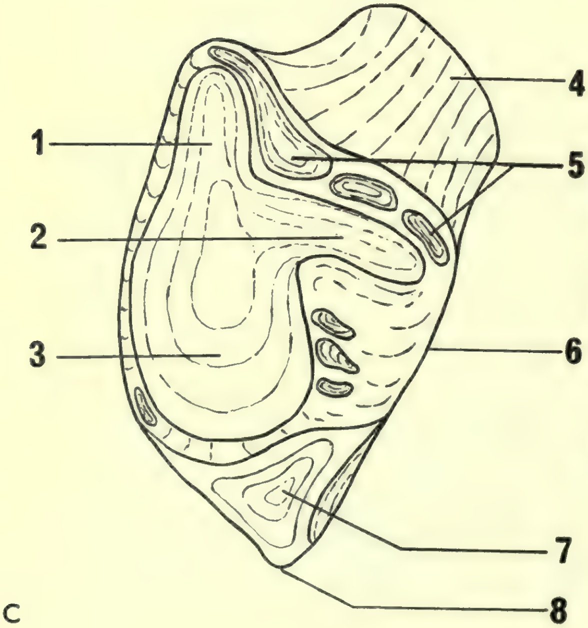
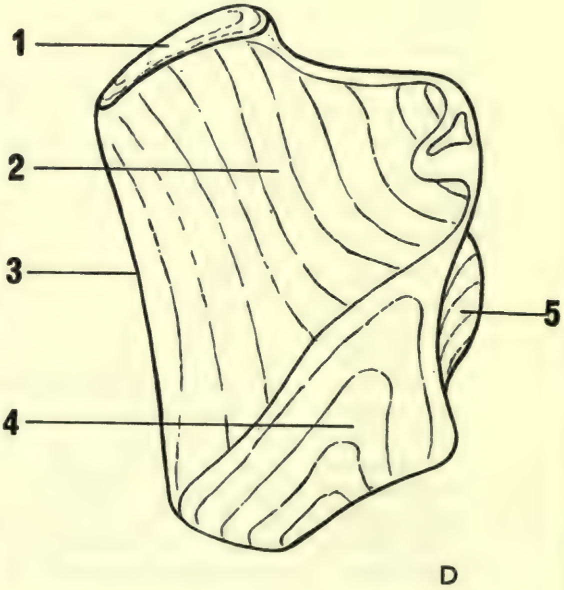
FIG. 4. (a). Supraoccipital, posterior view, ×2 (Evans' nodule). 1, dorsal edge. 2, foramen, which probably transmitted endolymphatic duct. 3, exoccipital facet. 4, triangular depressed area surrounding foramen. 5, roof of foramen magnum. (b). Supraoccipital, anterior view, ×2 (Evans' nodule). 1, grooved dorsal edge. 2, depressed areas of lateral surface. 3, impression of membranous labyrinth. 4, foramen. 5, grooved and pitted margin circumscribing membranous impression. 6, exoccipital facet. 7, roof of foramen magnum. (c). Supraoccipital, ventral view, ×2 (Evans' nodule). 1, posterior surface. 2, exoccipital facet. 3, membranous impression. 4, roof of foramen magnum.

second is fairly wide, directed toward the outer edge of the bone, and lies in the horizontal plane marking the position of the horizontal semicircular canal. In some specimens there is the slightest indication of a depression at the point of union of the two canals, marking the position of the ampulla of the anterior vertical semicircular canal. The internal surface of the bone is marked by fine striations similar









to those seen in the opisthotic, but here they are not quite so prominent. The entire margin of the proötic is grooved and pitted and is thinner than that of the opisthotic.

B. *Ossifications of the Mandibular and Hyoid Arches*

The mandibular and hyoid arches have an origin and development separate from the chondrocranium, but certain parts become so intimately associated with it that they form an integral part of the skull.

The mandibular arch is of two parts, the palatoquadrate bar above, and the mandibular bar, or Meckel's cartilage, below. Meckel's cartilage has but a single ossification, the articular, and the lower jaw is formed largely from the dermal elements which become applied to it. For convenience the articular will be described together with the other lower jaw elements in a later and separate section. The palatoquadrate has two ossifications in tetrapods, an anterior epiptyerygoid, and a posterior quadrate, the latter articulates with the articular of the lower jaw. Both elements form an integral part of the skull, and are therefore described in the present section.

The hyoid arch has a number of ossifications. Dorsally there is a single element, the stapes, whilst ventrally are elements which constitute the hyoid apparatus. Since the latter structure, unlike the stapes, does not form part of the skull, it is dealt with elsewhere.

1. *Stapes* (fig. 7, plate 2a). The stapes is located at the back of the skull and forms a strut between the opisthotic and basioccipital proximally, and the quadrate distally. Essentially the element comprises of a rounded head which bears a facet for articulation with the opisthotic, and a shaft which has an angulate bend directed ventrally. Distally the shaft widens, and terminates in an oblique and elongate articular surface which faces forwards and outwards, and which corresponds with a facet on the quadrate which faces obliquely backwards and inwards.

FIG. 5. (a). Opisthotic (left), posterior view, ×3 (Evans' nodule). 1, paroccipital process. 2, external lateral surface. 3, basioccipital facet. 4, ventral tip, part of which locates in a facet on the stapes. (b). Opisthotic (left), external view, ×3 (Evans' nodule). 1, impression of the posterior portion of the utriculus (or possibly the origin of the posterior vertical semicircular canal). 2, impression of horizontal semicircular canal. 3, grooved and pitted margin circumscribing membranous impression. 4, ventral depression, probably marking the position of a lagena. 5, paroccipital process. 6, external lateral surface. (c). Opisthotic (left), anterior view, ×3 (Evans' nodule). 1, impression of dorsal portion of the utriculus, or possibly of the posterior vertical semicircular canal. 2, impression of the horizontal semicircular canal. 3, impression of the sacculus. 4, paroccipital process. 5, grooves in margin circumscribing membranous impression. 6, external edge. 7, ventral depression probably marking the position of a lagena. 8, ventral tip. (d). Opisthotic (left), internal view, ×3 (Evans' nodule). 1, paroccipital process. 2, internal surface. 3, posterior edge. 4, basioccipital facet. 5, impression of sacculus.

The head of the stapes is stout and moderately well rounded, although it does tend to become raised dorsally into a low ridge which appears more prominent in mature specimens (R8177). On the posterior aspect there is a groove which runs obliquely forward and upward and which in life carried forward the stapedial artery. The stapedial groove is not always a prominent feature, and is most clearly seen in R8177. Above the level of the stapedial groove the head is no longer rounded, and, as mentioned before, it tends to be drawn up into a low ridge. The greater part of this dorsal portion is occupied by a shallow and triangular depression for the reception of the ventral tip of the opisthotic. While there is a certain degree of demarcation between upper and lower portions of the head, at least in mature forms, and while the dorsal portion has articular contact with the opisthotic, whether or not it could be described as the dorsal process in the full sense is conjectural (compare with the structure of the stapes in *Ophiacodon*, Romer & Price 1940). There can be no doubt that the head of the stapes, being channelled by the stapedial groove, is the true footplate, and it seems reasonable to conclude that the portion lying above the groove and articulating with the opisthotic could represent the true dorsal process.

While the anterior aspect of the head in R8177 is virtually devoid of feature, in the smaller specimens it is occupied by a shallow concavity (fig. 7d, 4). When the stapes is articulated with the reconstructed skull this facet is observed to be directed towards, and lie very close to the position now thought to have been occupied by a lagena. Since this facet lies in such a position it is concluded to be that part of the footplate which in life attached to the fenestra ovalis.

Whilst the dorsal edge of the shaft follows a gentle curve, the ventral edge is sharply angulate and its apex, which is directed downwards, is roughened and may have been the origin of a muscle. Similar rugosities occur on the anterior surface of

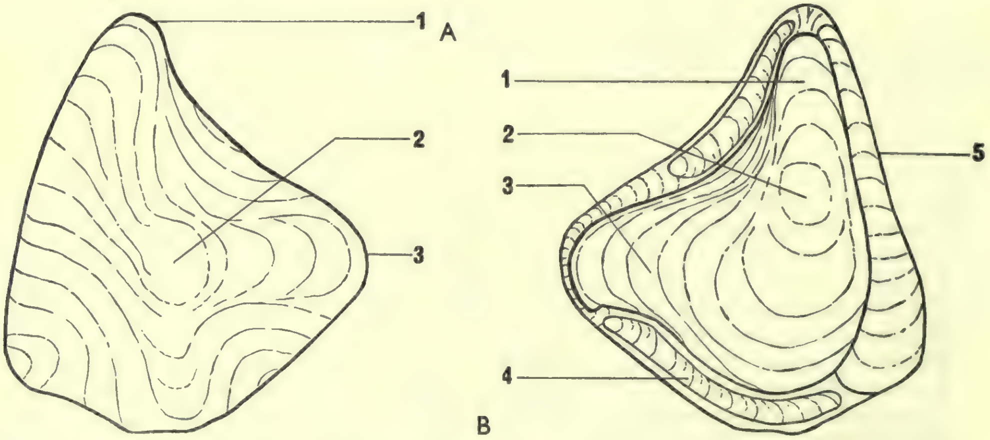


FIG. 6. (a). Proötic (left), anterior view, ×3, (Evans' nodule). 1, dorsal tip. 2. 'umbo'. 3, outside edge. (b). Proötic (left), posterior view, ×3 (Evans' nodule). 1, impression of anterior vertical semicircular canal. 2, probably the impression of an ampulla. 3, impression of the horizontal semicircular canal. 4, groove in margin of the bone which circumscribes the membranous impression. 5, internal edge.

the shaft, where it widens, and these are more prominent in some specimens than in others. The distal (quadrate) articular facet is slender and oval, and, facing forwards and outwards, its surface lies parallel with an oval depressed area on the posterior surface of the quadrate. It is quite smooth and sometimes slightly sunken so that the periphery is raised by a low lip. The quadrate depression is longer and wider than the facet of the stapes, and the two surfaces are separated by a gap so that it can safely be concluded that the stapes was continued distally in cartilage. The stapes must therefore have been an immobile strut between the quadrate distally and the otic capsule proximally.

2. *Epipterygoid* (fig. 8, plate 2b). Dorsally the epipterygoid enters into a complex and interdigitating suture with a descending process of the parietal, and has ventral contact with the pterygoid. The element therefore forms a strut between the skull roof and palate.

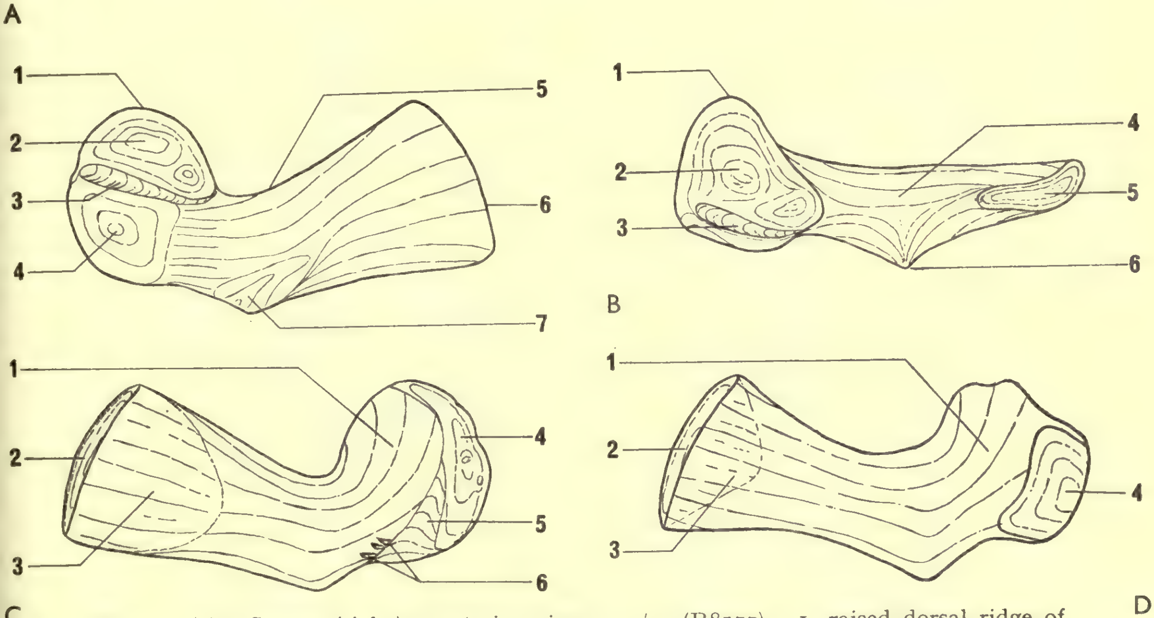


FIG. 7. (a). Stapes (right), posterior view, ×3/2, (R8177). 1, raised dorsal ridge of head. 2, postero-dorsal facet for reception of opisthotic. 3, groove marking course of stapedial artery. 4, rounded posterior surface of head. 5, dorsal edge of shaft. 6, distal edge of shaft. 7, raised bony ridge which may have been an area of muscle origin. (b). Stapes (right), dorsal view, ×3/2 (R8177). 1, raised dorsal ridge of head. 2, postero-dorsal facet for reception of opisthotic. 3, groove for stapedial artery. 4, dorsal edge of shaft. 5, distal facet of shaft which was in cartilaginous contact with the quadrate. 6, summit of raised bony ridge. (c). Stapes (right), anterior view, ×3/2, (R8177). 1, laterally inclined anterior surface of head. 2, distal facet. 3, shallow depressed area of bone, somewhat rugose. 4, slight indentation. 5, shallow groove. 6, denticular rugosities. (d). Stapes (right), from a smaller individual, anterior view, ×2, (based largely on R6697). 1, laterally inclined anterior surface of head. 2, distal facet. 3, area of rugose bone. 4, well marked facet on anterior aspect of head.

The epipterygoid bears superficial resemblance to a leg and foot, the toes of which rests in a shallow groove in the pterygoid, at the level of the basipterygoid articulation. The shaft, or 'leg', lies approximately in the vertical plane, and its external surface is grooved for about half its length. This groove is not single, however, because it is invaded by bony flanges dividing it into a number of longitudinal compartments. The medial surface of the descending parietal process is correspondingly ridged and grooved, and the two elements come together in a rigid interdigitating suture. The internal surface of the shaft has a less complex appearance and widens dorsally into a flange of bone which locates in a shallow depression high up on the medial surface of the epipterygoid process of the parietal.

The foot of the epipterygoid is laterally compressed and has a hollowed external surface due to the fact that the 'heel' is turned out. The internal surface of the foot is consequently convex. Medially, at the place where the foot joins the shaft (i.e. at back of the 'ankle'), the surface of the bone is rugose, the extent of the roughening

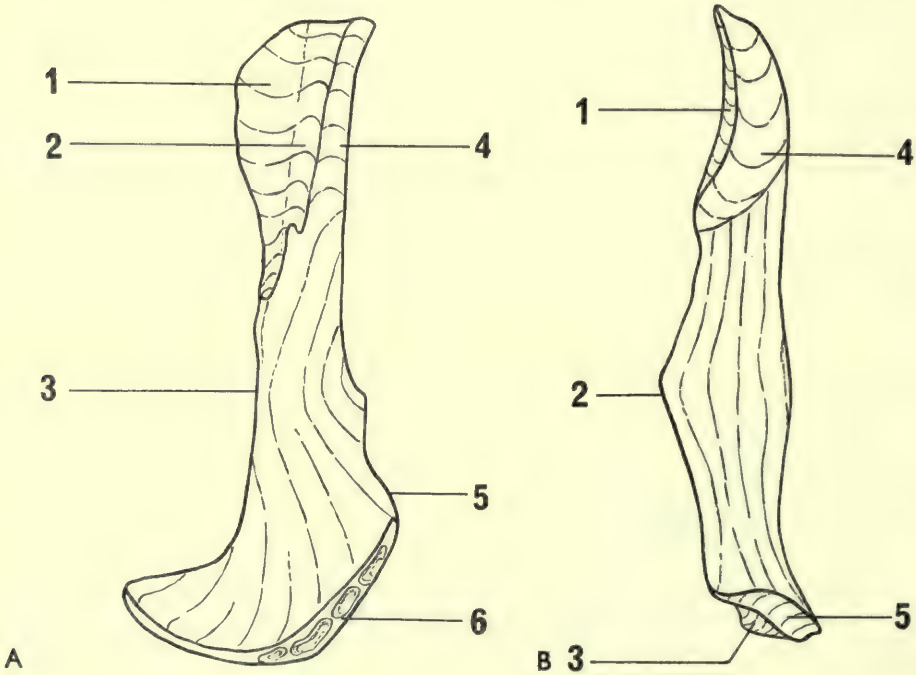


FIG. 8. (a). Epipterygoid (left), external lateral view, ×3/2 (R1168). 1, bony flange which locates in an ovoid facet on the medial surface of the descending epipterygoid process of the parietal. 2, deep edge groove for reception of the medial edge of the descending epipterygoid process of the parietal. 3, leading edge of shaft. 4, shallow groove. 5, posterior edge of foot which is turned outwards. 6, grooved and pitted ventro-lateral trailing edge of foot. (b). Epipterygoid (left), anterior view, ×3/2 (R1168). 1, medial surface of shaft produced into a smooth flange. 2, position of rugosity of the medial surface of the shaft. 3, medial surface of foot. 4, antero-medially inclined groove. 5, grooved and pitted ventral edge of foot.

varying from specimen to specimen. In some individuals (Evans' nodule) the rugosities are barely noticeable, whilst in others (R8177) they are very prominent, and the significance of this is discussed later (see *Kinesis*, below). The ventral trailing edge of the foot is grooved and depressed, indicative of cartilaginous continuity. The ventral portion of the leading edge of the quadrate has a similar

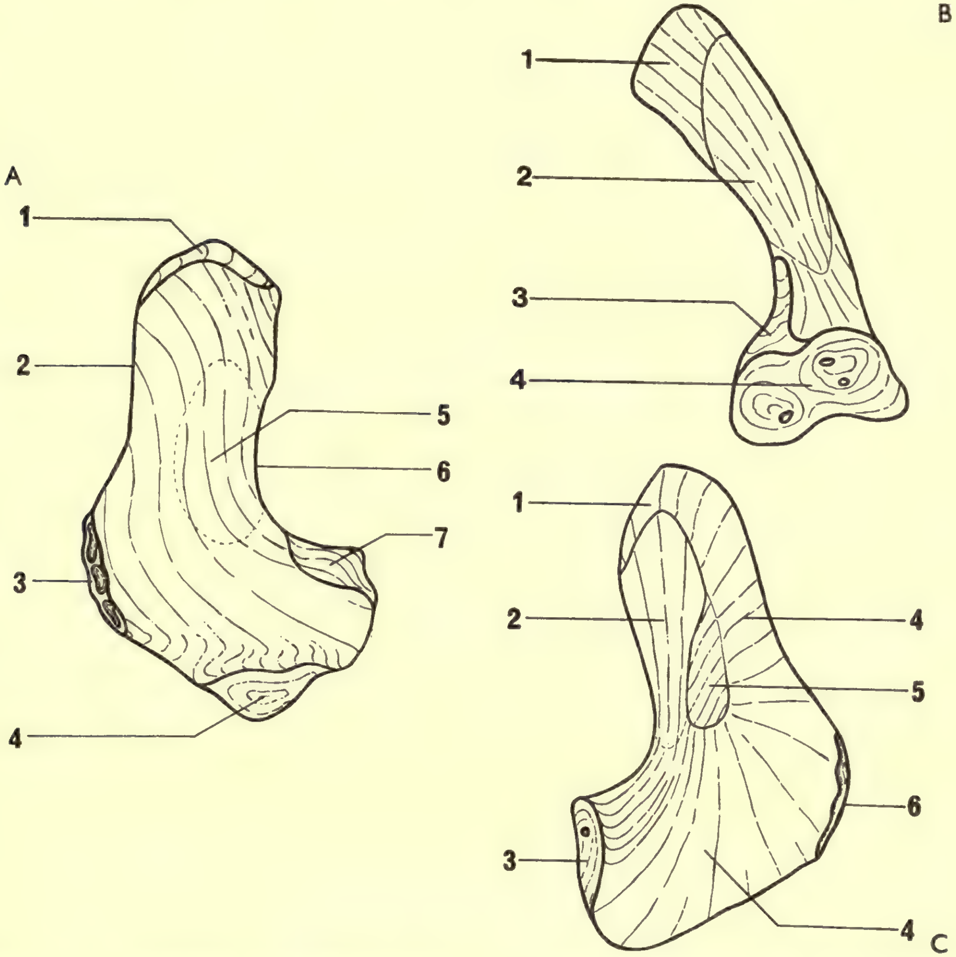
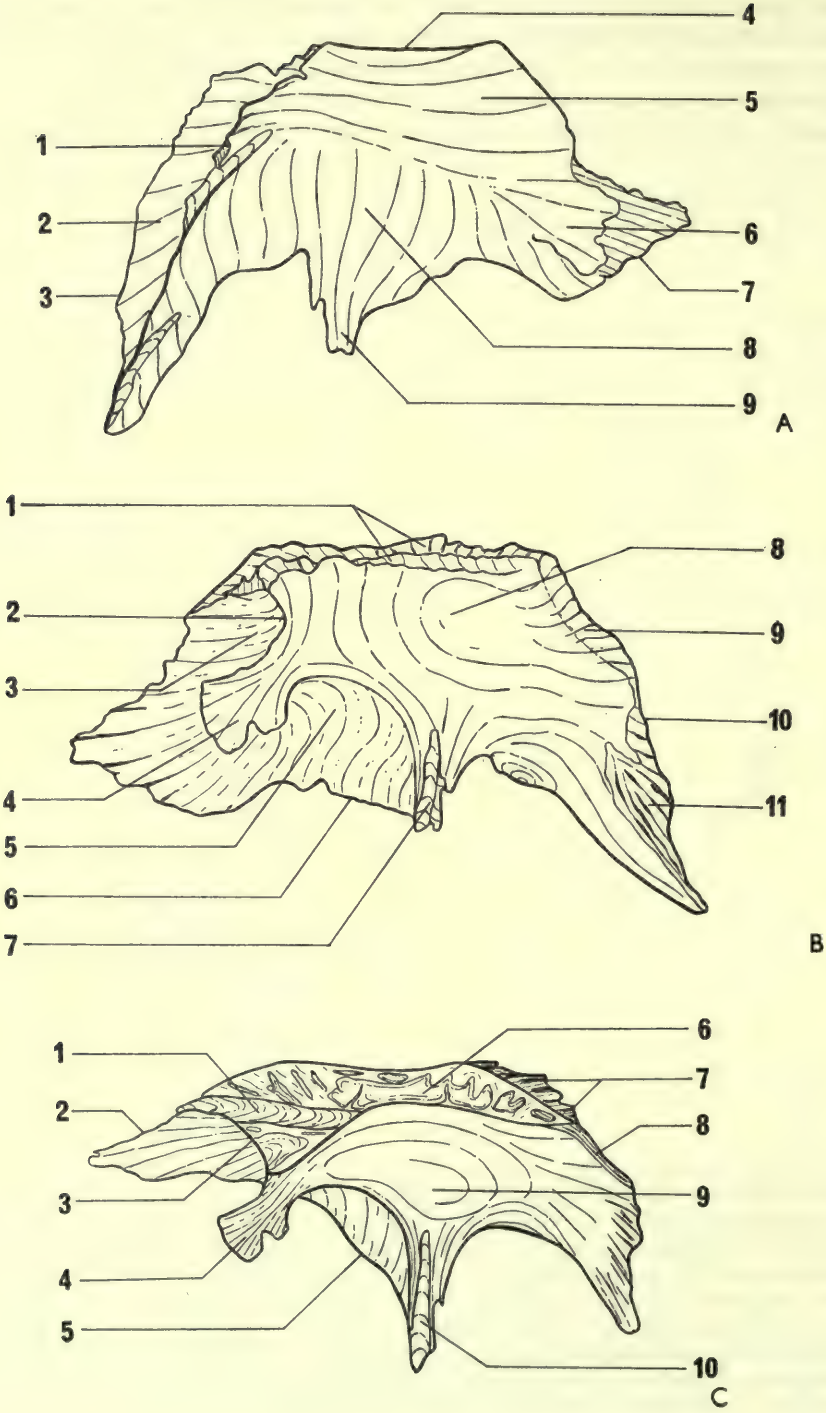


Fig. 9. (a). Quadrate (left), anterior view, just more than natural size (R6697). 1, grooved dorsal edge. 2, medial edge which slots into a groove in the squamosal. 3, pitted leading edge which was in cartilaginous continuity with the epipterygoid. 4, condyle. 5, area of origin of the *M. adductor mandibulae posterior*. 6, emarginated external edge. 7, quadratojugal facet. (b). Quadrate (left), external view, just more than natural size (R6697). 1, smooth facet of the external surface. 2, roughened area of the external surface. 3, quadratojugal facet. 4, condyle. (c). Quadrate (left), posterior view, just more than natural size (R6697). 1, smooth facet of external surface. 2, roughened area of external surface. 3, condyle. 4, posterior surface. 5, facet for reception of cartilaginous portion of stapes. 6, pitted leading edge.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appearance, and lies close behind the epipterygoid, and it is concluded that the two elements were joined in life by cartilage.

The ventral edge of the foot is continued anteriorly where it ascends and becomes inflected forming a narrow shelf of bone (a 'toe-cap').

3. *Quadrate* (fig. 9, plate 2c). The quadrate is a relatively large element which has dorsal contact with the squamosal, medial contact with the pterygoid, and articulates with the lower jaw ventrally through the articular. Anteriorly it probably had cartilaginous continuity with the epipterygoid.

In anterior view the quadrate resembles an external ear flap, having a reniform outline, and being hollowed. In most specimens examined there is an oval area of bone (shown by a broken line in fig. 9a), where the surface is sculptured, and this probably marks the origin of the *M. adductor mandibulae posterior*. Since the bone is relatively thin the posterior surface tends to have a shape corresponding to the anterior surface, but is angulate rather than convex, forming two flat surfaces set at right angles to one another. For much of its length the dorsal portion therefore has an L-shaped section. The wider of these two faces is inclined backwards and inwards, and makes medial contact with the quadrate wing of the pterygoid. Contact does not involve the whole of this surface however, and posteriorly there is an oval and slightly depressed area which had cartilaginous continuity with the distal facet of the stapes.

The external edge is emarginated and contributes with the posterior edge of the quadratojugal in the formation of an elliptical foramen. On the external surface on some specimens a smooth dorsal facet is marked off from a roughened ventral portion, as shown in fig. 9b.

The quadrate thickens ventrally forming the articular condyle. In ventral view the condyle is triangular, tapering medially, and its anterior border which curves gently, continues the line of the intrapterygoid vacuity without interruption. The ventral surface of the condyle, which bears a triangular depression, curves upwards

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FIG. 10. (a). Parietal (right), dorso-lateral view, just less than natural size (R8177). 1, parietal ridge. 2, bony shelf extending back from parietal ridge. 3, posterior edge. 4, dorsal edge. 5, depressed area of dorsal surface. 6, Bony lamella. 7, anterior edge. 8, descending lateral wall. 9, epipterygoid process. (b). Parietal, ventral view, just less than natural size (R8177). 1, bony lamellae of median dorsal edge. 2, transverse ledge forming the anterior margin of the optic lobe impression. 3, impression marking posterior portion of the cerebral hemisphere. 4, parietal flange. 5, extra-encephalic impression. 6, external lateral edge. 7, groove in epipterygoid process for reception of epipterygoid. 8, impression of optic lobe. 9, shallow depression marking position of cerebellum. 10, posterior edge. 11, rugosities. (c). Parietal (right), internal lateral view, just less than natural size R8177. 1, deep groove in median dorsal edge into which slots the postero-lateral edge of the frontal. 2, anterior edge. 3, impression marking posterior portion of the cerebral hemisphere. 4, parietal flange. 5, external lateral edge. 6, lamellate depression of median dorsal edge. 7, rugosities on median side of parietal ridge. 8, impression marking position of cerebellum. 9, impression of optic lobe. 10, groove in epipterygoid process.

externally and is continuous with the lateral surface, and it is only this portion which enters into articulation with the mandible. In external view, the articular surface of the condyle appears almost round. Just above the articular surface, at the anterior and external corner of the condyle, there is an oval bony protuberance circumscribed by a groove, and this receives the hollow articular facet of the quadratojugal.

DERMAL BONES

The dermal elements of the skull will be considered under four headings, those forming the skull roof and temporal arcade, the bones of the circumorbital series, the bones of the palate and upper jaw margin, and the sclerotic elements. The quadratojugal does not fall into any of these groups, but will be placed for convenience with the circumorbital elements, and the palatine, which is an element of mixed origin, is included with the dermal elements of the palate. Since the lower jaw is an integral structure which does not separate into individual elements, it is not possible to figure and describe the elements separately in the same way as those of the skull. The descriptions of the lower jaw will therefore be given in a separate section.

A. *ELEMENTS OF THE SKULL ROOF AND TEMPORAL ARCADE*

1. *Parietal* (fig. 10, plate 3a). The parietal is a massive element which forms the hind portion of the skull roof, and the medial margin of the temporal vacuity. That the mandibular muscles take direct or indirect origin from the parietal is reflected in the thickness of its walls, and in its various rugosities. Anteriorly it articulates with the frontal, and has contact with the prefrontal and with the postfrontal; posteriorly it articulates with the squamosal, and ventrally with the epipterygoid.

In dorsal view the parietal has the appearance of a trapezium, with its shorter side lying medially and its long side sloping steeply down forming the external lateral surface. The anterior edge is inclined to the longitudinal axis, being directed forwards, and terminates in an acute point. The posterior edge is also inclined, but faces backwards and inwards, and also curves ventrally. Running parallel with the posterior margin, and just anterior to it, is a very prominent and rugose crest which is referred to as the parietal ridge, and which articulates distally with the squamosal. The shelf of bone which extends back from the parietal ridge is relatively thin, and probably made contact with the dorsal margin of the supraoccipital.

The descending lateral wall is drawn out midway along its length into a tapering finger of bone which enters into a complex sutural union with the epipterygoid, and which is described as the epipterygoid process. In advance of the epipterygoid process the lateral margin slopes gently upward to meet the anterior margin, and behind it describes an arc, the leading edge of which runs approximately parallel with the parietal ridge. The parietal ridge thus marks the dorsal edge of a solid trigonid which curves downwards postero-laterally. The ventral surface of the parietal bears impressions of certain cerebral structures, and it is necessary to describe them in some detail, but the discussion of their significance is postponed till later.

The most prominent of the encephalic impressions lies at the level of the epipterygoid process, is ovoid, relatively deep, and has its longitudinal axis approximately parallel with that of the skull. This impression is concluded to be that of the optic lobe of the brain. The anterior margin is formed by an almost straight and transverse ledge which is the ventral edge of a prominent buttress of bone formed by the thickening of the leading anterior edge of the parietal. Laterally the buttress is drawn out into a spatulate flange of bone which descends ventro-laterally with its flat ventral surface facing downwards and inwards. This flange, which probably gave support to the large optic lobe, is described as the parietal flange. The external lateral margin of the optic lobe impression is formed in part by the medial surface of the epipterygoid process. Caudally this is continued by a ridge which curves in towards the midline and which also forms the posterior margin. Rostrally the lateral margin is formed by a bony lip, which is also the medial margin of a deep and lateral extra-encephalic concavity, and which is continuous with the external edge of the descending parietal flange. The medial margin of the optic lobe impression is formed by the slightly raised ventro-medial edge of the parietal, and its posterior margin lies close to the posterior edge of the element, separated by a narrow ledge of bone which bears evidence of a second and far less well defined impression.

The second encephalic impression is very shallow and can easily be overlooked. It is slender, and approximates to a crescent, with the concave edge towards the posterior margin of the parietal. Caudally the impression tapers to a slender point. With its neighbour of the other side, and the ventral surface of the supraoccipital, it forms a single depression which embraced the cerebellum.

Immediately dorsal in position to the proximal portion of the parietal flange is an undercut which continues forward as a fairly shallow depression. This excavation contributes with a depression in the frontal element in the embrace of the cerebral hemisphere. The posterior medial corner of this excavation is much broken up by an area of pits and depressions of unknown significance. This third encephalic impression is narrower than that of the optic lobe but is perhaps just deeper.

The extra-encephalic depression is equally as deep as that of the optic lobe impression, but shallows anteriorly. The external lateral margin is formed by the internal lateral surface of the parietal and is bounded posteriorly by an almost vertical wall of bone which is continuous with the anterior surface of the epipterygoid process.

The medial edge of the parietal has a considerable depth and is relatively straight when viewed from above, but in ventral view is seen to follow an uneven path. The edge is not flat, but is broken up by a number of plates which interdigitate with those of the opposite edge when the parietals are articulated, thus forming a rigid suture.

2. *Frontal* (fig. 11, plate 3b). The frontal is a relatively small and delicate element which contributes to the skull roof, and which embraces the pineal foramen. For its greater part it is overlain by the nasal, and its postero-lateral edge slots into a recess in the leading dorsal edge of the parietal.

In dorsal view the frontal is somewhat crescentic. The external edge curves towards the mid-line both in front and behind, whilst the medial edge is straight for most of its length. Posteriorly, however, the medial edge bears an ovoid emargination which borders the pineal foramen. The dorsal surface is strongly arched from side to side, corresponding to the encephalic excavations of the ventral surface. The anterior edge follows an S-shaped course, whilst the posterior edge follows a smooth convex curve.

The ventral surface bears two depressed areas; one circumscribes the pineal foramen and is the deepest, the other occupies the remainder of the surface and is shallow. The deep posterior depression is crescentic, and is interpreted as marking the position of the cerebral hemisphere. In the antero-medial corner of the cerebral hemisphere impression there is a prominent pitted area of unknown significance, similar to that seen in the parietal. The anterior excavation is separated from the one behind by a low ridge, and is concluded to be the impression of the olfactory lobe. This impression is shallow, and flattens out anteriorly.

3. *Nasal* (fig. 12, plate 3c). The nasal is a stout element which contributes to the skull roof posteriorly, and to the dorsal surface of the snout anteriorly. It has an overlapping contact with the frontal and prefrontal posteriorly, lateral contact with the lachrymal, and is overlapped anteriorly by the premaxilla. With the premaxilla and lachrymal it participates in the formation of the external narial aperture.

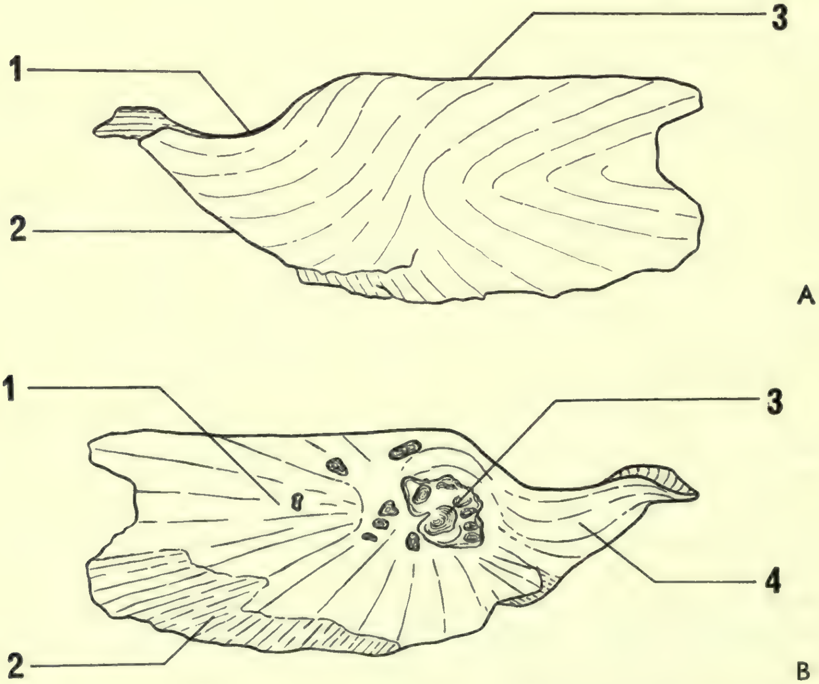


Fig. 11. (a). Frontal (right), dorsal view, ×4/3 (R8177). 1, lateral margin of pineal foramen. 2, postero-lateral edge. 3, medial edge. (b). Frontal (right), ventral view, ×4/3 (R8177). 1, shallow depressed area marking the position of the olfactory lobe. 2, roughened area of bone. 3, foraminous area. 4, deep crescentic depression marking the position of the cerebral hemisphere.

Since the nasal is preserved in the prepared material only up to the level of the external narial aperture, the rest of its structure must be inferred from the study of serial sections and unprepared skulls, and the present description is therefore somewhat incomplete.

The nasal is essentially a rectangular strip of bone, the external edge of which is turned down anteriorly, giving an L-shaped cross section. Before tapering posteriorly, the lateral surface is drawn out into a descending triangular process, which, being slightly outward-inclined, makes lateral contact with the medial surface of the prefrontal. Posterior to this level, the nasal is substantially flat, and tends to become splayed out. The divergent appearance is in part caused by a series of divergent ridges and striations which mark the dorsal surface of the bone. Furthermore there is a triangular depression in this posterior region which is flanked on either side by the divergent ridges. Up to this level the medial edge of the nasal is quite straight, and the two elements lie in flush contact on either side of the midline. Anteriorly,

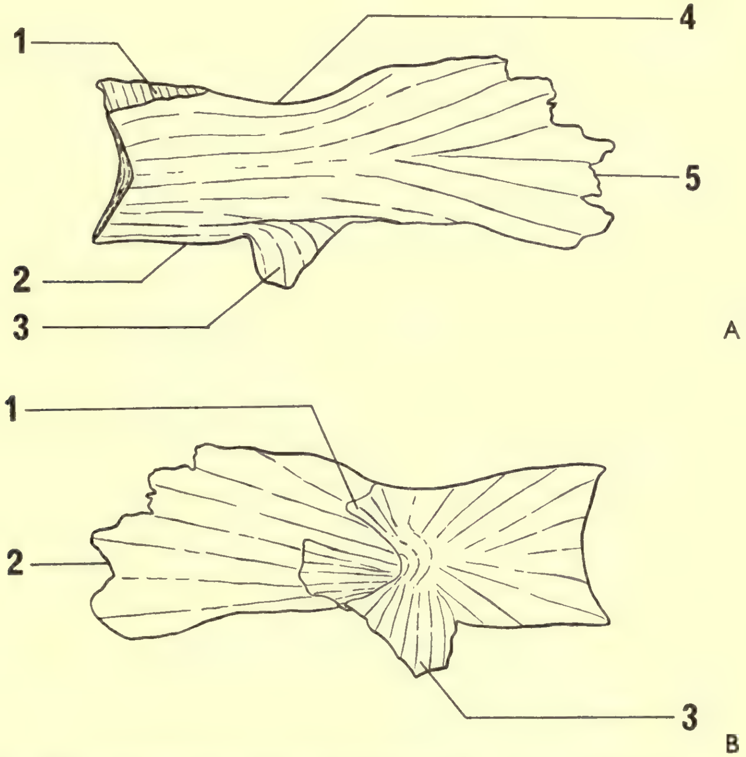
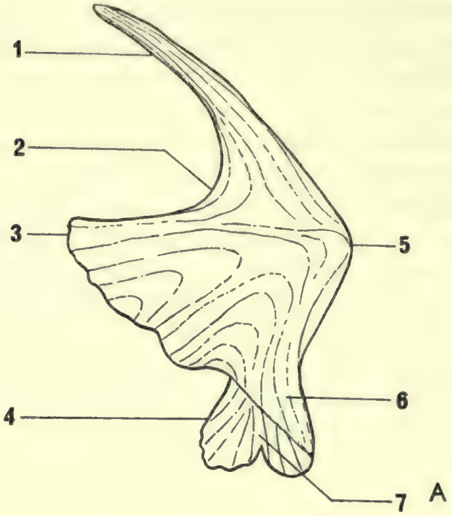


FIG. 12. (a). Nasal (left), dorsal view, slightly less than natural size (R8177). 1, articular facet for reception of the neighbouring nasal element. 2, external edge. 3, descending triangular process. 4, shallow emargination of medial edge which borders the internasal foramen. 5, posterior edge. (b). Nasal (left), ventral view, slightly less than natural size (R8177). 1, backwardly projecting bony spur. 2, posterior edge. 3, descending triangular process.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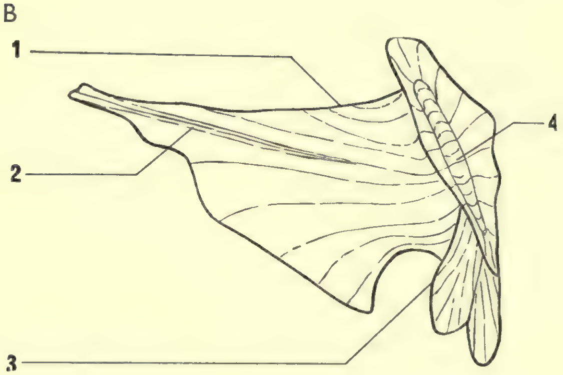
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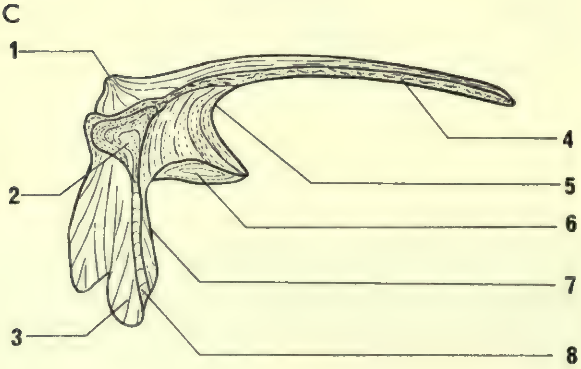
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however, the medial edge of each nasal has a shallow emargination, and the dorsal surface of the bone is depressed in this region. An internasal foramen is thus formed when the elements are articulated, and this is circumscribed by a shallow and elliptical depression. The bony edge of the emargination is thin, but thickening rostrally it becomes excavated, forming an articular facet for the reception of the corresponding edge of the other nasal bone.

The ventral surface is relatively smooth, but is roughened where it overlaps the frontal. Medially, just posterior to the emargination, there is a backwardly projecting bony spur. Into the angle of this spur slots part of the anterior edge of the frontal.

4. *Squamosal* (fig. 13, plate 6f). The squamosal is a tripartite element whose three rami lie approximately in the three planes of space. Forming the lateral and posterior margins of the temporal vacuity the squamosal has contact with the postfrontal anteriorly, the parietal posteriorly and medially, the quadrate posteroventrally, and the postorbital and quadratojugal laterally.

From above the dorsal margin is J-shaped, the long arm being formed by the lateral ramus, the other by the much shorter medial ramus. Both rami increase in depth caudally, and thus have triangular profiles, and their external surfaces bear striations which converge upon a bony protuberance posteriorly. The protuberance is the most posterior point of the element, and lies just below the level of the rim of the vacuity. In addition to these striations, the external surface of the lateral ramus bears a number of low ridges which are also convergent upon the protuberance. Tapering anteriorly, the lateral ramus rests in a long and depressed facet on the postfrontal.

The medial ramus, being relatively short, is quite blunt, and has the appearance of an equilateral triangle when viewed from the side. The base of the triangle is directed obliquely forwards and downwards, and is furled out forming a semilunar hollow which embraces the distal portion of the parietal ridge.

The internal surface of the squamosal is hollow and relatively smooth, and its deepest portion corresponds with the protuberance of the outer surface. The internal surface of the lateral ramus is raised by a ridge, which, diminishing in its prominence posteriorly, disappears before reaching the centre of the depression.

The third ramus, the ventral ramus, is continuous with the medial one, and is directed downwards and inwards. It is a bifid flange of bone, which is set obliquely

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FIG. 13. (a). Squamosal (right), postero-dorsal view, ×2/3 (R8177). 1, lateral ramus. 2, rim of temporal vacuity. 3, medial ramus. 4, leading edge of ventral ramus. 5, bony protuberance. 6, ventral ramus. 7, medial surface of ventral ramus. (b). Squamosal (right), ventro-medial view, ×2/3 (R8177). 1, dorsal rim of temporal vacuity. 2, ridge on internal surface of the lateral ramus. 3, leading edge of ventral ramus. 4, depression at distal end of medial ramus. (c). Squamosal (right), ventro-lateral view, ×2/3 (R8177). 1, bony protuberance. 2, depression in angle between lateral and ventral rami. 3, external surface of ventral ramus. 4, ventral edge of lateral ramus. 5, dorsal rim of temporal vacuity. 6, depression at distal end of medial ramus. 7, leading edge of ventral ramus. 8, vertical groove.

to the longitudinal axis of the skull so that its external surface faces forwards as well as outwards. The external surface of the leading edge of the ventral ramus is grooved throughout its length and this groove slopes backward so that its distal end lies in advance of its proximal end. Dorsally this groove opens into a ventrally directed depression which is excavated in the angle between the lateral and ventral rami. Into this depression fits the dorsal edge of the quadrate, while much of its leading edge slots into the longitudinal groove of the ventral ramus. Both internal and external surfaces of the ventral ramus bear fine longitudinal striations which converge proximally.

B. *THE CIRCUMORBITAL SERIES*

The orbit is bounded by the prefrontal and postfrontal dorsally, the postorbital posteriorly, the jugal ventrally, and the lachrymal anteriorly. The postfrontal also

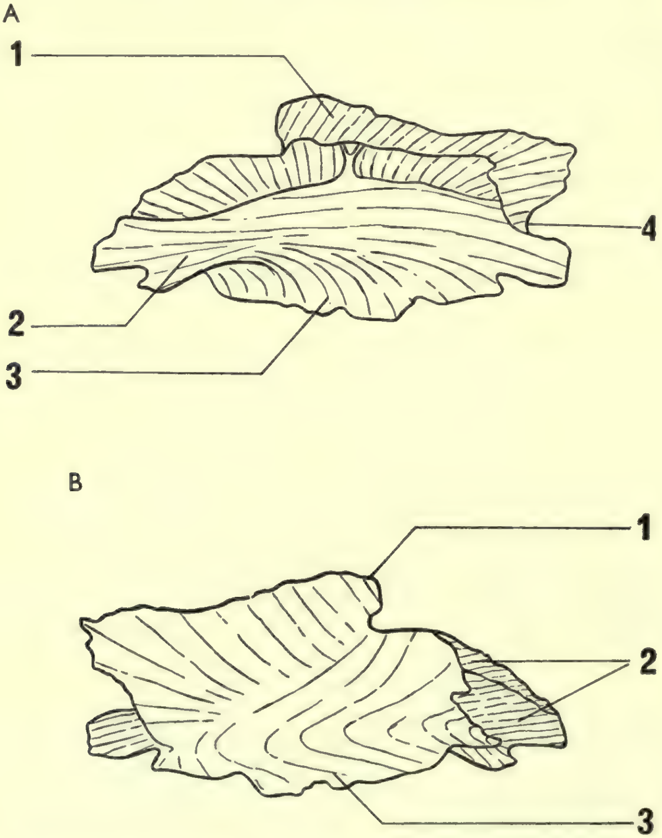


FIG. 14. (a). Prefrontal (right), ventral view, natural size (R8177). 1, medial flange. 2, midrib. 3, lateral flange. 4, posterior edge. (b). Prefrontal (right), dorsal view, natural size (R8177). 1, medial flange. 2, vertical bony lamellae ascending from anterior portion. 3, lateral flange.

participates in the formation of the temporal vacuity. The quadratojugal has no part in the formation of the orbit, but will for convenience be described here.

1. *Prefrontal* (fig. 14, plate 3e). The prefrontal is a narrow and curving element whose concave ventral surface contributes to the anterior dorsal margin of the orbit. Ventrally it articulates with the lachrymal, posteriorly with the parietal and postfrontal, and mesially with the nasal and frontal.

From below, the prefrontal comprises of a smooth and arched midrib, from which the bone tapers on either side forming a lateral and a medial flange. The midrib is rounded from side to side, and, with the smooth lateral flange, forms the anterior dorsal margin of the orbit. The medial flange is lamellate, and partly underlapped by the frontal and parietal, and makes a minor contribution to the skull roof. Anteriorly both lateral and medial flanges taper so that only the midrib makes ventral contact with the lachrymal. The two flanges also taper posteriorly.

The dorsal surface is very much roughened, and much of it is overlapped by the postfrontal. The lateral and medial margins of the prefrontal are both raised above the level of the midrib so that the dorsal surface is furrowed, and has a somewhat V-shaped cross section.

2. *Postfrontal* (fig. 15, plate 3d). The postfrontal is a dorso-ventrally compressed element which forms the posterior dorsal margin of the orbit. Medially it contributes

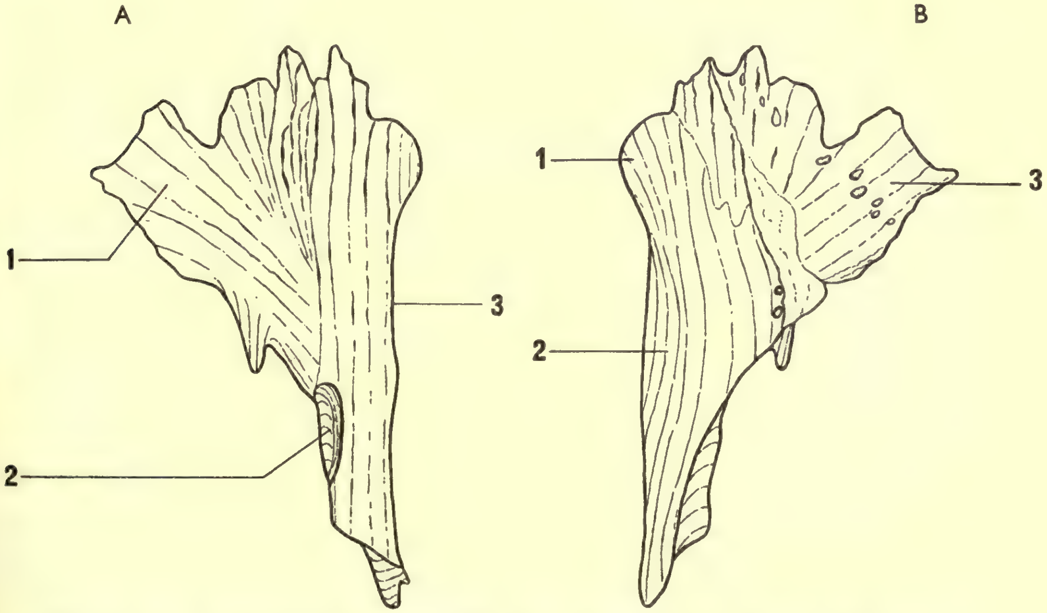


FIG. 15. (a). Postfrontal (right), dorsal view, just less than natural size (R8177). 1, medial limb. 2, squamosal facet. 3, dorso-lateral edge. (b). Postfrontal (right), ventral view, just less than natural size (R8177). 1, triangular area of smooth bone. 2, orbital margin. 3, medial limb.

to the temporal vacuity, and also forms part of the skull roof. It overlaps the prefrontal anteriorly, the nasal anteriorly and medially, and the parietal posteromedially. Posteriorly it articulates with the squamosal and also has contact with the postorbital.

Seen from above the postfrontal is Y-shaped, the two short limbs being directed rostrally. Of these, the medial one is narrowest, and set at an oblique angle to the other, which is continuous with the main limb, and which lies parallel with the longitudinal axis of the skull. While the dorsal surface of the medial limb is finely striated, that of the wide limb is thrown into prominent folds and is marked by coarse striations. The dorsal surface of the main limb is fairly smooth and is arched in correspondence with the line of the orbit. Furthermore it is twisted so that posteriorly it comes to lie almost in the vertical plane. Posteriorly and medially it is excavated by a long and oval facet for reception of the squamosal.

The ventral surface, save for a triangular area of smooth bone which borders the orbit, is rugose, and is applied to the similarly roughened dorsal surface of the prefrontal. The external margin of the orbital area is concave from side to side and becomes slightly convex medially, towards the apex of the triangle.

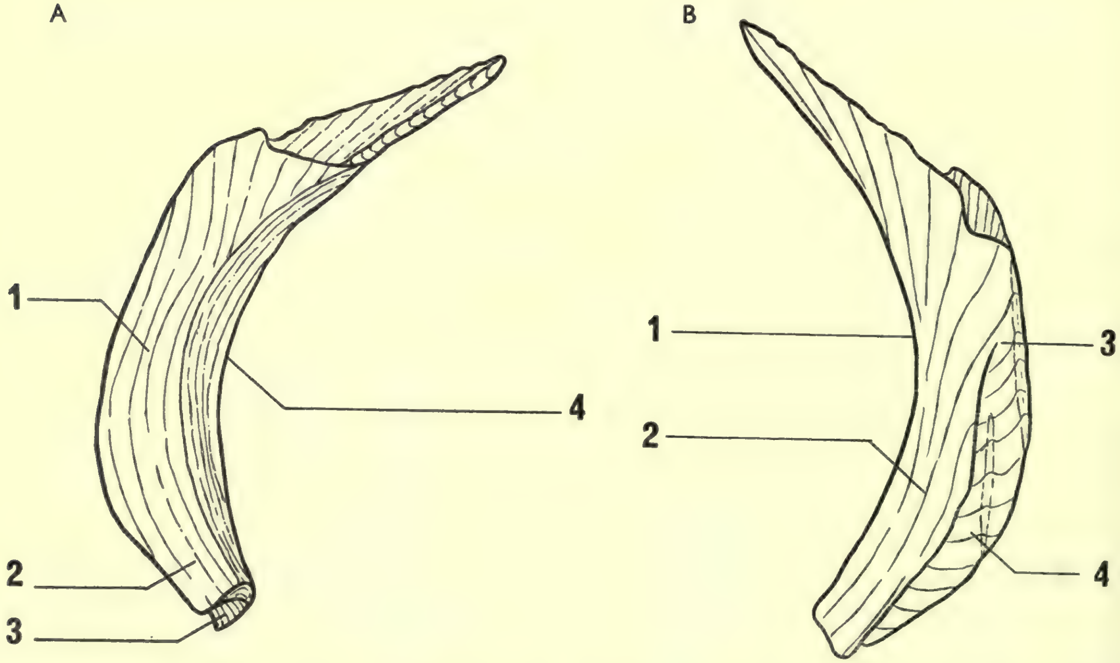


FIG. 16. (a). Postorbital (right), external lateral view, ×3/2 (based on R6697 and R8177). 1, convex external surface. 2, external plate. 3, internal plate. 4, sharp anterior edge. (b). Postorbital (right), internal lateral view, ×3/2 (based on R6697 and R8177). 1, sharp anterior edge. 2, internal plate. 3, commencement of fissure. 4, external plate.

Due to poor preservation posteriorly, the precise nature of its articulation with the postorbital cannot be ascertained. However sufficient information has been provided by specimen R8177 to show that a dorso-laterally inclined and roughened area of the postorbital made contact with, and was overlain by, a similarly roughened but ventro-lateral area of the postfrontal.

3. *Postorbital* (fig. 16, plate 4a). The postorbital is not well preserved in the material examined, and the following description is based upon two specimens, (R8177 and R6697), neither of which is complete. The bone is slender and sickle-shaped, its curving anterior edge forming the posterior border of the orbit. Posteriorly it articulates with the quadratojugal, ventrally with the jugal, while dorsally it has contact with the postorbital, presumably in an overlapping relationship.

The external surface is not flat, but is convex from before to behind. The anterior

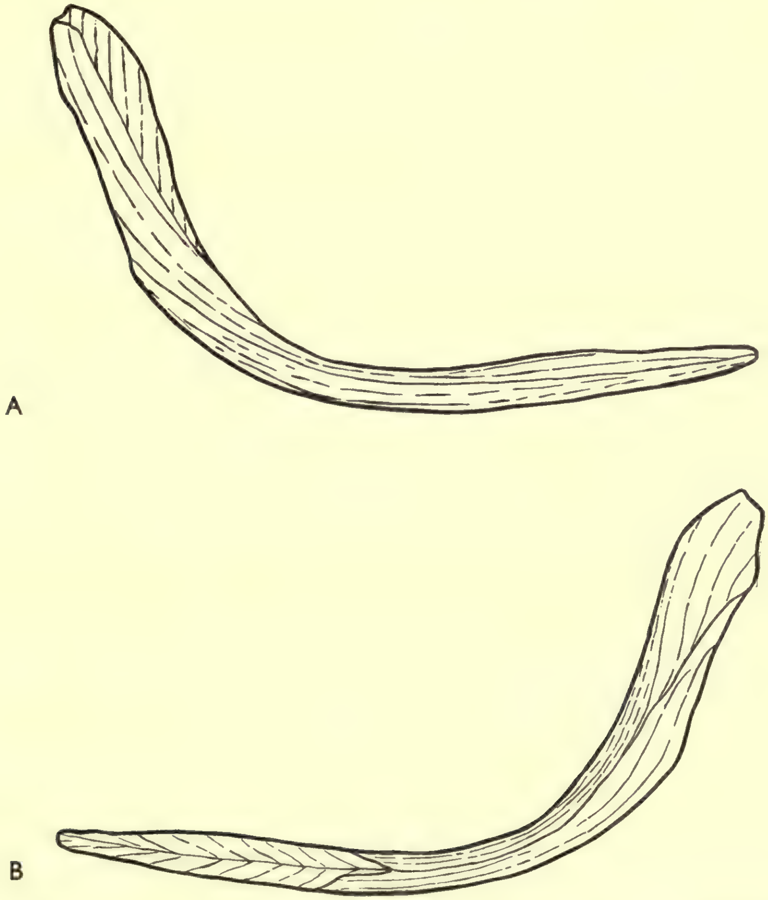


Fig. 17. (a). Jugal (right), external lateral view, slightly less than natural size (R8177).
(b). Jugal (right), internal lateral view, slightly less than natural size (R8177).

border follows a concave path, and the convexity of the external surface results in its having a sharp edge for much of its length. Dorsally and ventrally the sharpness is reduced, and gives way to rounded margins.

For much of its length the trailing edge of the element is divided by a fissure into two bony plates, one external, the other internal. The fissure commences high up on the medial surface of the element as a shallow groove, lying approximately midway between the anterior and posterior margins, and about one third of the way down from the dorsal edge. Widening as it deepens ventrally, the fissure separates the internal and external plates by a moderate gap. Most of the fissure is occupied by the leading edge of the quadratojugal, but ventrally it embraces the dorsal edge of the terminal portion of the jugal.

The internal surface of the postorbital is slightly concave from side to side, and therefore corresponds to the convexity of the external surface, but the portion forming the internal plate is quite flat.

4. *Jugal* (fig. 17, plate 4d). The jugal is a slender and gently curving element which forms the ventral, and part of the posterior border of the orbit. Posteriorly it articulates with the postorbital and it also has contact with the quadratojugal. Antero-medially it articulates with the maxilla, whilst its tip locates in a groove formed between the maxilla and lachrymal.

Although slender, the jugal is quite robust, and has an ovoid or triangular cross-section over much of its length. Sloping gently upwards anteriorly it becomes laterally compressed and finally tapers to a slender splint which locates in the groove above-mentioned.

Much of the anterior half is triangular in cross-section, with a fluted medial surface rising to the apex and articulating with a correspondingly sculptured area of bone on the posterior lateral surface of the maxilla. Caudally the cross-section becomes rounded, and dorso-ventrally compressed where the jugal forms the mid-portion of the orbital floor. As the jugal curves up to contribute to the posterior margin of the orbit it becomes laterally compressed and terminates in a moderately flat flange of bone which makes contact with the quadratojugal, and whose dorsal edge slots into the postorbital fissure.

5. *Lachrymal* (fig. 18, plate 4c). The lachrymal forms the anterior corner of the orbit, articulating dorsally with the prefontal, and ventrally with the jugal and maxilla. The rectangularity of its sharp leading edge and the arcuation of its broad internal margin confers the appearance of the prow of Viking boat.

The internal orbital margin is relatively smooth, and its ascending dorsal limb is convex from side to side. Ventrally the orbital margin is concave and its width is increased by a flange of bone which arises from the external surface of the bone. Dorsally, at its widest point, this bony flange loses contact with the rest of the external surface and is produced as a biramous tongue.

The external surface, although ridged, is relatively flat, whereas the internal surface is much roughened and thrown into folds and ridges. A prominent ventro-

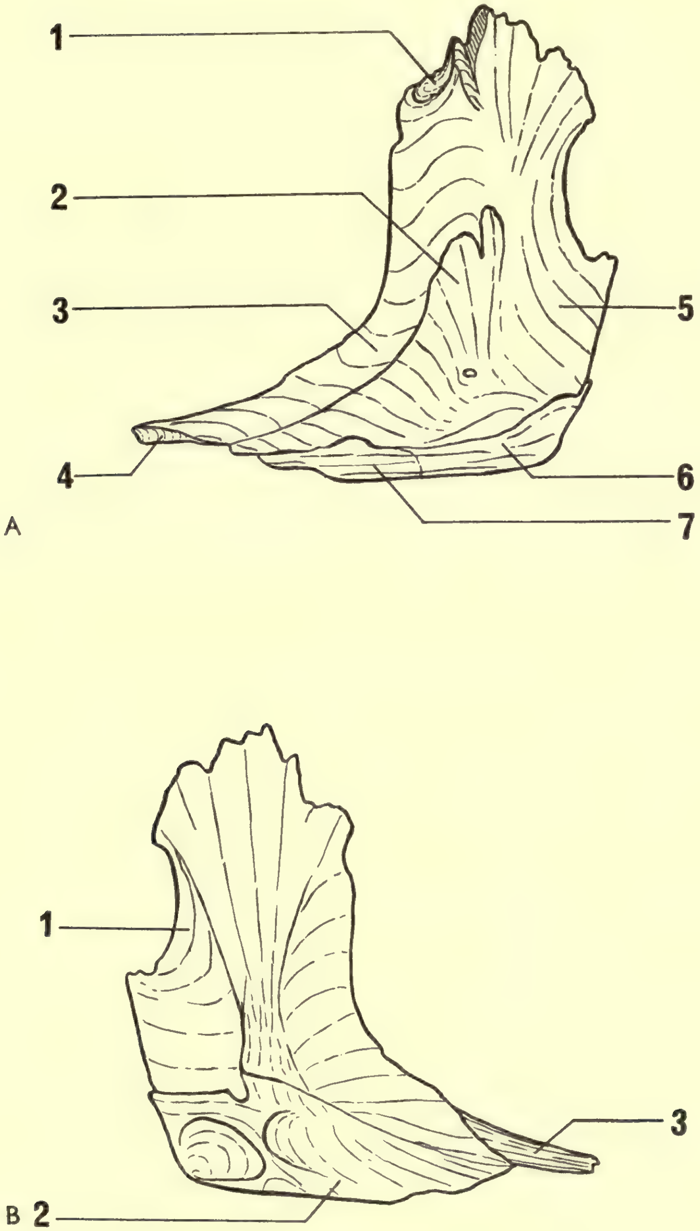


Fig. 18. (a). Lachrymal (right), external lateral view, slightly more than natural size (R8177). 1, prefrontal facet. 2, bony flange. 3, orbital margin. 4, posterior portion of ventro-lateral furrow. 5, anterior vertical plate. 6, ventral horizontal plate. 7, jugal facet. (b). Lachrymal (right), internal lateral view, slightly more than natural size (R8177). 1, anterior vertical plate. 2, ventral horizontal plate. 3, ventral portion of orbital margin.

lateral furrow articulates with a corresponding ridge on the dorsal surface of the maxilla.

Beyond the orbital margin the bone diminishes rapidly in its thickness, and is reduced to two thin plates, one anterior and vertical, the other ventral and horizontal. In the posterior corner of the ventral plate there is a small oval depression into which locates the anterior tip of the jugal.

The Quadratojugal (fig. 19, plate 4b). The quadratojugal is known from only three specimens, and is somewhat incomplete in each case so that this description suffers certain shortcomings.

Occupying a posterior and lateral position in the skull the quadratojugal articulates ventrally with the quadrate, and anteriorly with the postorbital and jugal. As mentioned above, part of its posterior margin contributes with the quadrate in the formation of a postero-lateral foramen of moderate size.

A thin and triangular element, the quadratojugal has something of the appearance of a mammalian scapula, its ventral quadrate articular facet corresponding with the glenoid fossa. The internal surface is smooth and hollow, whilst the external surface is convex and bears a prominent vertical ridge set a little way back from its anterior margin. This ridge curves over antero-laterally forming a groove into

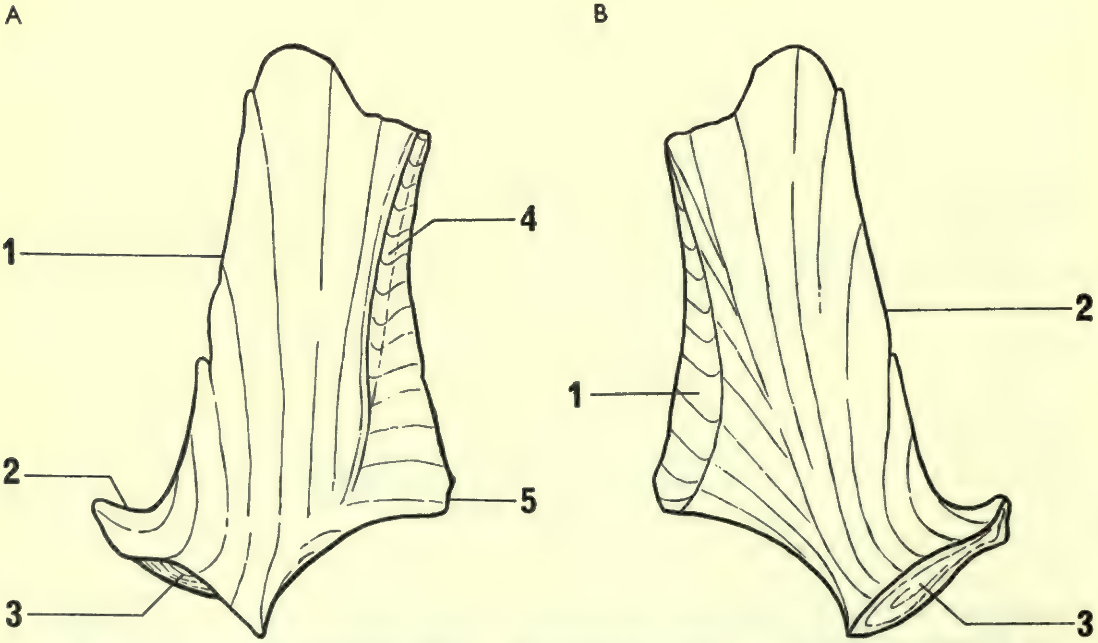


FIG. 19. (a). Quadratojugal (right), posterolateral view, × 2, R6697. 1, posterior margin. 2, spur. 3, quadrate facet. 4, groove into which the postorbital slots. 5, apex of leading edge. (b). Quadratojugal (right), internal lateral view, × 2, R6697. 1, postorbital facet. 2, posterior margin. 3, quadrate facet.

which slots the external posterior edge of the postorbital. A little way in front of this ridge is a second, though lesser one (in R8177), against which rests the posterior edge of the jugal. In specimen R6697 this ridge is not present.

Dorsally the quadratojugal widens out like a fan, while ventrally it becomes constricted, only to fan out once more to form an elliptical articular facet. Ventrally the facet is hollow, and articulates with a swelling on the quadrate which is shaped for its reception.

The leading edge of the quadratojugal is triangular and its longest side lies above the apex and slots into a deep fissure in the posterior region of the postorbital. The trailing edge is quite straight for most of its length, but ventrally it is produced into a slightly upturned and curved spur, which forms the floor of the oval foramen.

C. *ELEMENTS OF THE PALATE AND UPPER JAW MARGIN*

The palate is formed from the paired pterygoids, palatines, and vomers, with a minor contribution from the single and median parasphenoid. The upper jaw margin is formed largely from the premaxillae, the maxillae contributing to the posterior portion. Both maxilla and premaxilla are grooved and dentigerous. The descriptions of the palatal elements are based largely upon a single specimen, R8177.

1. *Pterygoid* (fig. 20, plate 5a). The pterygoid is an extensive element which makes a major contribution to the formation of the palate. Anteriorly it articulates with the vomer, posteriorly with the epipterygoid and quadrate, and medially with the basisphenoid, whilst much of its external margin is overlapped by the palatine.

Essentially the pterygoid is a tapering sheet of bone which is widest and thickest posteriorly where it is produced into three winged processes. Anteriorly the bone undergoes torsion so that the dorsal surface turns outwards finally becoming the external surface of a narrow terminal rod.

Two of the three triangular winged processes lie in approximately the same plane forming an extensive shelf which, facing obliquely upwards and outwards, makes contact over a wide area with the medial surface of the quadrate. This articular surface is referred to throughout as the quadrate wing of the pterygoid. The third wing is directed medially and somewhat ventrally, and rests with the dorsal aspect of its tip in touch contact with the ventral edge of the basioccipital. This process is referred to as the medial wing. For the most part the dorsal surface of the medial wing is rugose but becomes smooth anteriorly and forms the floor of an ovoid excavation, into which the basipterygoid process of the basisphenoid locates. Immediately anterior to this facet the internal edge of the pterygoid is emarginated and forms the interpterygoid vacuity (or internal palatal foramen), which is separated from its neighbour on the other side by the parasphenoid. Just posterior to this level there is a similar emargination of the external edge which constitutes the intrapterygoid vacuity (or external palatal foramen), and which, lying directly beneath the temporal vacuity, served for the passage of the mandibular adductor muscles. On the dorsal surface, at the anterior corner of the intrapterygoid vacuity, there is a small crescentic articular facet for the palatine.

On the dorsal surface, just medial in position to the intrapterygoid vacuity, there is a short longitudinal groove which receives the tip of the epipterygoid and which probably marks the position of the cartilaginous portion of the palato-quadrate bar, as noted by Appleby (1961, 339). In line but not in continuity with this groove, there is a shallow furrow extending almost the length of the element and which might also mark the position of the cartilaginous palatoquadrate.

Tapering gently from the level of the emarginations the pterygoid is produced

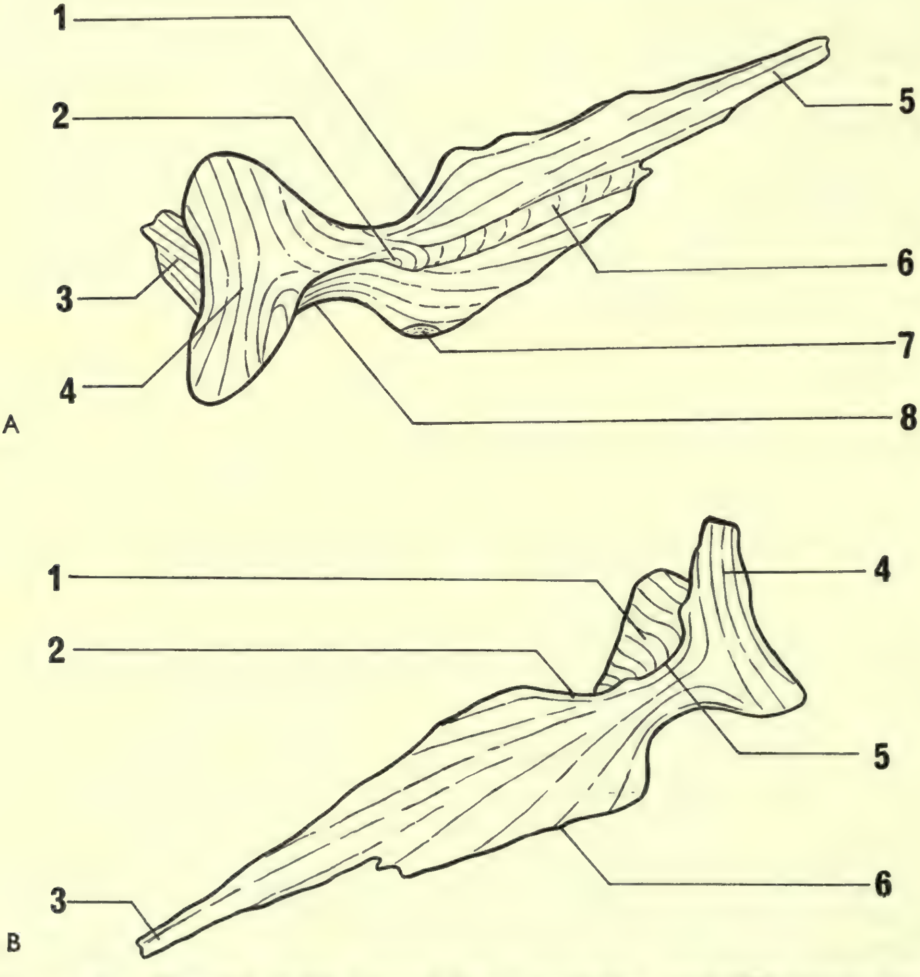


FIG. 20. (a). Pterygoid (right), external dorso-lateral view, × 1/2 (R8177). 1, edge of interpterygoid vacuity. 2, epipterygoid facet. 3, dorsal surface of medial wing. 4, quadrate wing. 5, external surface of terminal rod. 6, shallow furrow. 7, palatine facet. 8, intrapterygoid vacuity. (b). Pterygoid (right), ventro-medial view, × 1/2 (R8177). 1, medial surface of quadrate wing. 2, edge of interpterygoid vacuity. 3, longitudinal furrow. 4, ventral surface of medial wing. 5, ventral lip of basipterygoid facet. 6, external edge.

anteriorly into a narrow rod of bone. The medial and ventral surfaces of this rod are grooved and somewhat reticulate, though this may be due to damage, while the lateral surface is quite smooth and slightly furrowed, and has medial articular contact with the vomer.

The anterior portion of the dorsal surface of the pterygoid bears a low ridge which runs close to and approximately parallel with the lateral edge. This ridge has contact along its length with the medial edge of the palatine.

2. *Palatine* (fig. 21, plate 5b). The palatine is a relatively large and delicate bone which forms the outer margin of the palate, and has medial contact with the pterygoid throughout its entire length. Laterally it has contact with the maxilla for much of its length.

Rhombic in outline, the two long sides lie parallel with the longitudinal axis, and are raised above the level of the rest of the bone, producing a shallow basin. The posterior edge lies at almost 45° to the longitudinal axis, and slopes back so that the internal corner lies posterior to the external corner. The anterior edge lies very approximately parallel with the posterior edge, but tapers gradually to an oblique point.

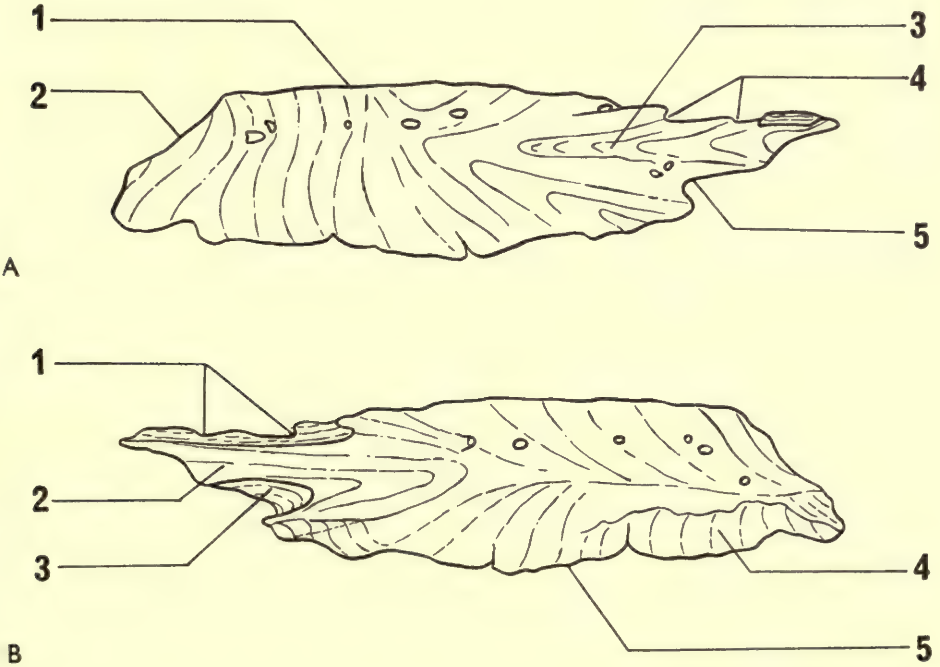


FIG. 21. (a). Palatine (left) dorsal view, × 3/4, (R8177). 1, external edge. 2, posterior edge. 3, longitudinal furrow. 4, vascular foramina. 5, margin of internal narial aperture. (b). Palatine (left), ventral view, × 3/4 (R8177). 1, vascular foramina. 2, medial surface of ventral keel. 3, margin of internal narial aperture. 4, pterygoid facet. 5, internal edge.

The dorsal surface is sculptured by various rugosities and striations and anteriorly is thrown into a prominent longitudinal furrow. Since the bone is so thin this furrow affects the ventral surface which is correspondingly produced into a keel. Anteriorly there is an ovoid excavation which is more prominent when viewed from beneath, and which contributes with the vomer in the formation of the internal narial aperture. Ventrally this excavation forms the medial boundary of the keel. The outer edge of the ventral keel has several fenestrations which correspond with similar fenestrations of the medial edge of the maxilla, with which articular contact is made. The foramina thus formed probably served to transmit blood vessels. For the most part the ventral surface is relatively smooth, but there is a posterior and medial area where the bone is lamellate, and applied to the dorsal surface of the pterygoid, but it is possible that this appearance is due to poor preservation.

A series of six foramina pierce the bone obliquely so that the dorsal aperture of each lies just posterior, though coincident, with the ventral aperture, and these probably transmitted blood vessels also.

3. *Vomer* (fig. 22, plate 5c). The vomer is the most anterior of the palatal elements and contributes with the palatine in the formation of the internal narial aperture. Externally, it has contact with the palatine, and for much of its length it is underlain by the pterygoid. Anteriorly the vomers of either side come into contact along their medial surfaces. Only the posterior portion of the element is adequately known from prepared material, but the remainder can be reconstructed by reference to part-prepared material and serial sections.

Posteriorly the vomer has a very pronounced ventral keel which is offset from the midline, lies towards the external margin, and makes medial contact with the pterygoid. The keel widens and becomes more shallow posteriorly so that it has the appearance of a raked stern of a ship. The dorsal surface in this region is concave, and the centre of its depression is towards the external margin which lies well below the level of the medial margin. The bone is thin, and for the most part is roughened and pitted.

The external lateral surface is quite smooth, convex from dorsal to ventral edges, and is gently incurved from before to behind. Anteriorly and dorsally there is an ovoid depression whose anterior margin is formed by an ascending bony spur and which is the medial margin of the internal narial aperture.

The medial lateral surface of the vomer is largely of cancellous bone, and is drawn out dorsally into a membranous overhang. Ventrally is a strip of relatively smooth bone which tapers posteriorly and which is the articular surface for contact with the pterygoid.

Anterior to the level of the internal narial aperture the dorsal aspect is produced into a thin vertical plate which reaches a maximum height then gradually tapers away. Anteriorly the vomer is reduced to a tenuous rod of bone which persists for a considerable distance, but it does not reach the tip of the snout.

4. *Parasphenoid* (fig. 1). As noted above, the parasphenoid is so intimately associated with the basisphenoid that its proximal limits are difficult to discern.

Anteriorly it is produced into a narrow strip of bone which lies in mid-ventral line between the pterygoids, making a minor contribution to the palate.

In the material so far examined the parasphenoid has been incompletely preserved and only the proximal portion is known.

5. *Maxilla* (fig. 23, plate 4e). The maxilla is known from only one prepared specimen (R8177), and only the posterior portion is preserved so that little can be said of its structure. Forming the posterior portion of the upper jaw margin, the maxilla has a dentigerous groove on its ventral surface. Contact with the palatine is made along the length of its medial margin, and the jugal rests in a groove on its external surface. Dorsally the maxilla has contact with the ventral surface of the lachrymal.

The dentigerous groove extends the full width of the ventral surface, and, diminishing in depth posteriorly, the element tapers to a blunt point. The medial margin of the dentigerous groove is perforated by a number of fenestrations which correspond with similar openings on the external margin of the palatine, as pointed out above. The dorsal surface is thrown into a number of prominent ridges which are separated by grooves. One of these ridges is particularly prominent and increases in width anteriorly forming a thin bony lamella against which the lachrymal abuts. The external surface gradually tapers to a point both before and behind, so that the element has the form of a slender wedge when the complete skull is viewed from the side.

6. *Premaxilla.* The premaxilla is an extensive element which forms the greater part of the snout and upper jaw margin. Since this element is not preserved in the prepared material at present available, its structure has been established by reference to unprepared skulls and serial sections.

The premaxilla commences at the level of the external narial aperture where it overlaps the anterior portions of the maxilla and lachrymal. Increasing in width rostrally, each premaxilla encroaches upon the nasal element of that side, and the nasals eventually disappear from view as the premaxillae meet above them in mid-dorsal line. The ventro-lateral edge of the premaxilla rapidly thickens rostrally forming the dentigerous upper jaw margin.

D. *THE SCLEROTIC RING* (fig. 24, plate 6e)

The sclerotic ring is composed of a variable number of individual plates, usually between 12 and 16, which come together in a complex sutural association. Each plate tapers towards its inner margin which is straight or slightly curved, whilst its outer margin, which is serrated, is invariably rounded. The sclerotic plate is not flat but is flexed at an angle of about 90° into an almost flat anterior surface, and a rounded lateral surface. The anterior surface contributes to the ring circumscribing the aperture, the lateral surface contributes to the lateral wall. The flat surface tends to be slightly hollow when viewed in profile, and its inner margin is somewhat raised. The elevation of the inner margin is accentuated by the inclination of the inner surface as it approaches the inner margin. The inner margin of the sclerotic ring is therefore

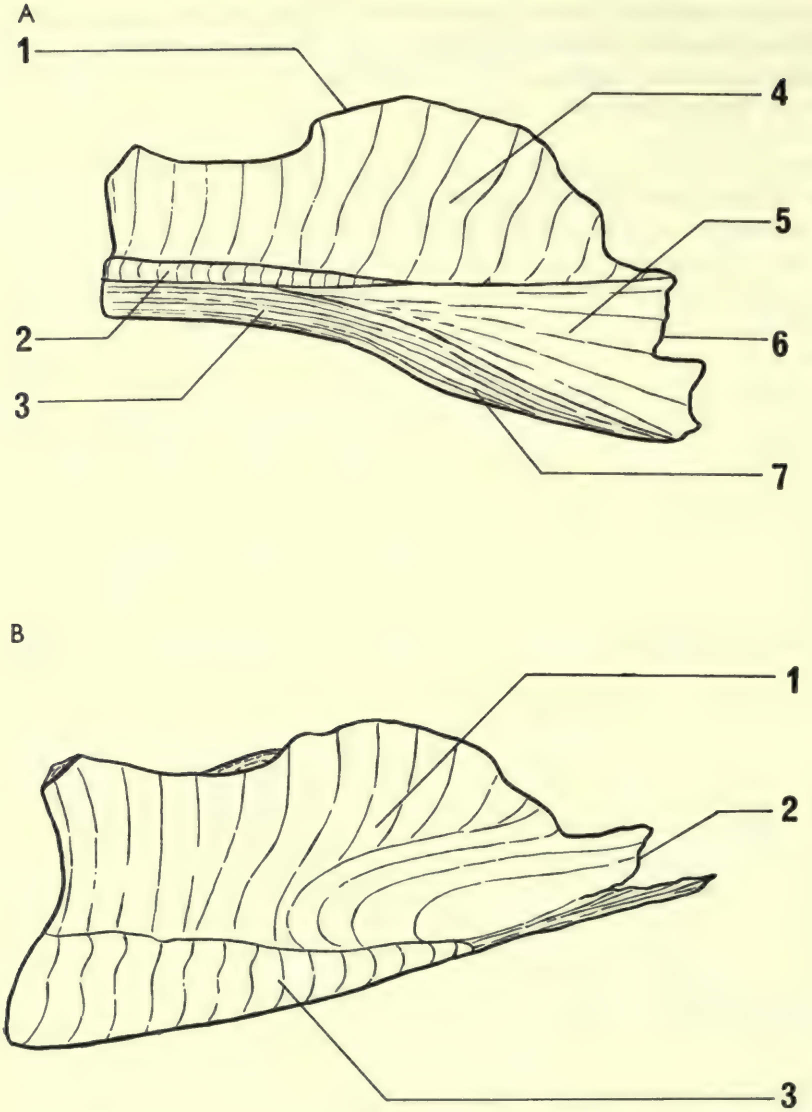
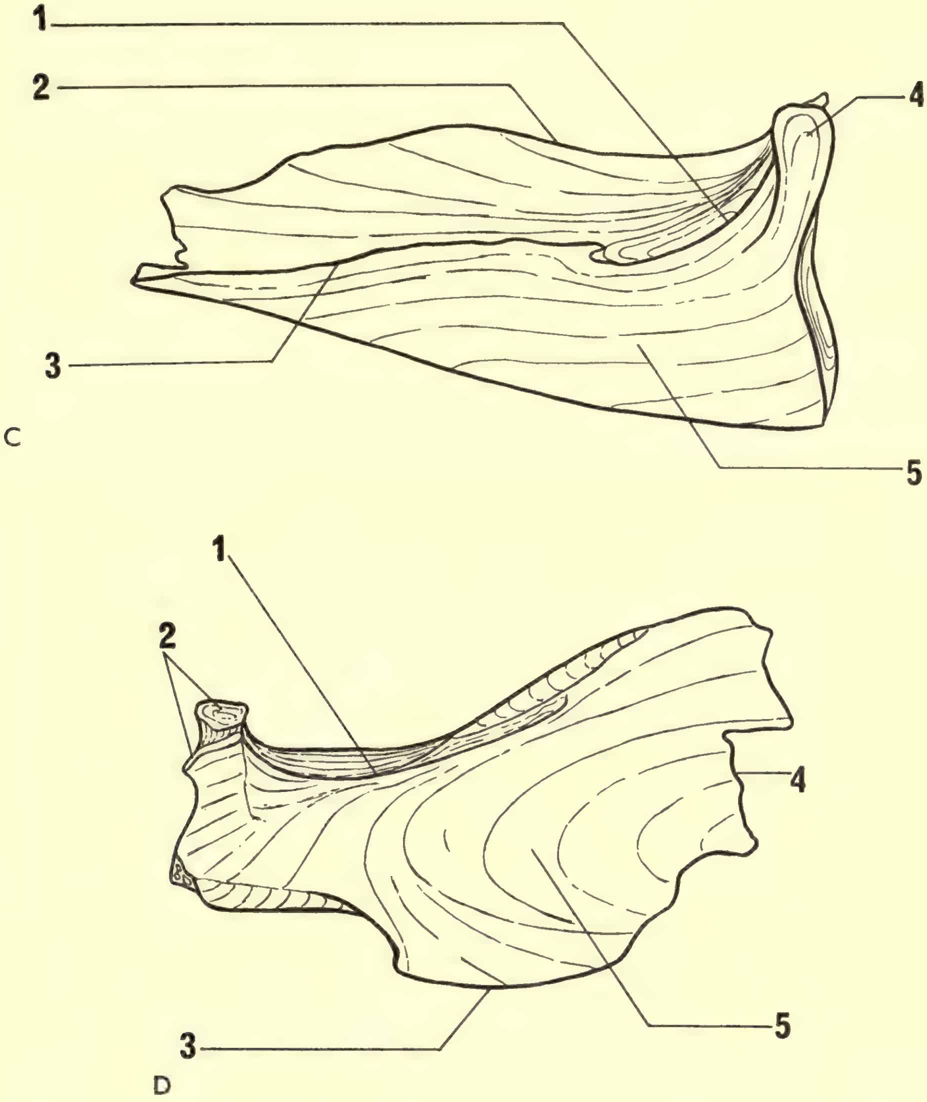


FIG. 22. (a). Vomer (right), ventral view, natural size (R8177). 1, medial edge. 2, pterygoid facet on medial surface of ventral keel. 3, external surface of ventral keel. 4, medial lateral surface. 5, ventral surface. 6, posterior edge. 7, external lateral surface. (b). Vomer (right), internal lateral view, natural size (R8177). 1, medial lateral surface. 2, posterior edge. 3, pterygoid facet of ventral keel. (c). Vomer.

raised very slightly, and thus circumscribed by a shallow suclus, the significance of which will be discussed later.

While the inner, (i.e. posterior), surface of the sclerotic plate is relatively smooth and flat, that of the outside is squamous and sculptured by fine and radiating striations.



(right), external dorso-lateral view, natural size (R8177). 1, medial margin of internal narial aperture. 2, medial edge. 3, external edge. 4, ascending bony spur. 5, external surface of ventral keel. (d). Vomer (right), dorsal view, natural size (R8177). 1, medial margin of internal narial aperture. 2, apex of ascending bony spur. 3, medial edge. 4, posterior edge. 5, hollowed dorsal surface.

Adjacent sclerotic plates come into contact at their lateral margins with little overlap but because of the interdigitation of the thin scales their simple arrangement is often obscured when the sclerotic ring is examined in its entirety. In specimen R8177, where the sclerotic ring has been well preserved, it can be seen that the plates

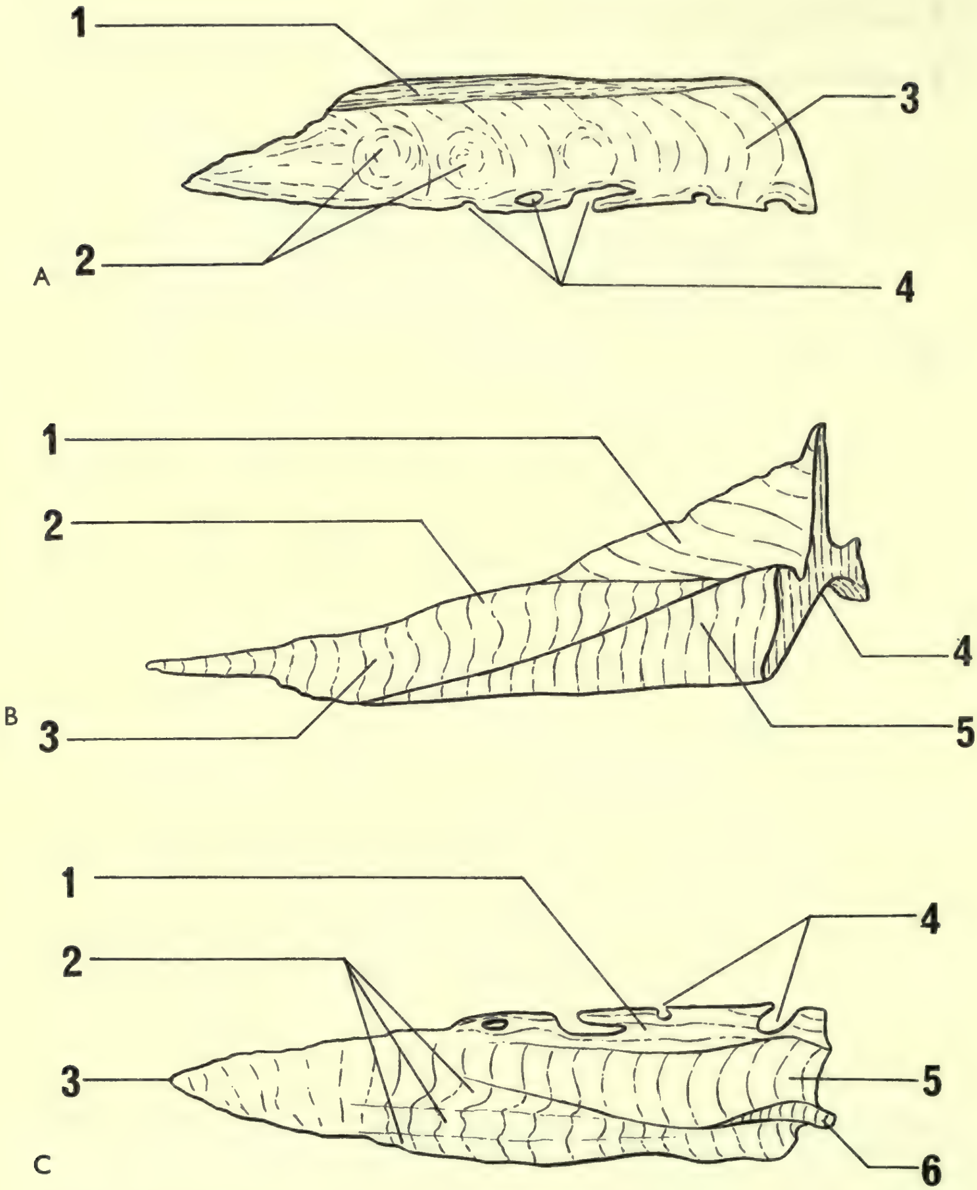


FIG. 23. (a). Maxilla (right), ventral view, ×3/2 (R8177). 1, external surface. 2, shallow dental alveoli. 3, dentigerous groove. 4, vascular foramina perforating medial margin. (b). Maxilla (right), external dorso-lateral view, ×3/2 (R8177). 1, bony lamella. 2, bony ridge which slots into a ventral groove in the lachrymal. 3, groove on dorsal surface. 4, dentigerous groove. 5, external surface. (c). Maxilla (right), dorsal view, ×3/2 (R8177). 1, palatine facet. 2, grooves on dorsal surface. 3, posterior tip. 4, vascular foramina perforating medial margin. 5, wide groove. 6, dorsal margin of bony lamella.

are arranged so that one lateral margin tends to overlap that of an adjacent plate, whilst the other is itself overlapped.

In those latipinnates so far examined, the aperture of the sclerotic ring tends to be relatively large in comparison with the size of the whole structure, and is usually slightly oval, the long axis being almost coincident with the longitudinal axis of the skull.

DESCRIPTION OF THE LOWER JAW

(Fig. 25, plate 6a)

With the exception of the articular and coronoid, (an element hitherto undescribed in the Ichthyosauria), the elements of the lower jaw are firmly united, and their true relationships have long been known and well documented in the literature. Much of the information has been obtained by studying sections where the individual elements usually retain their original relationships. It will not be necessary there-

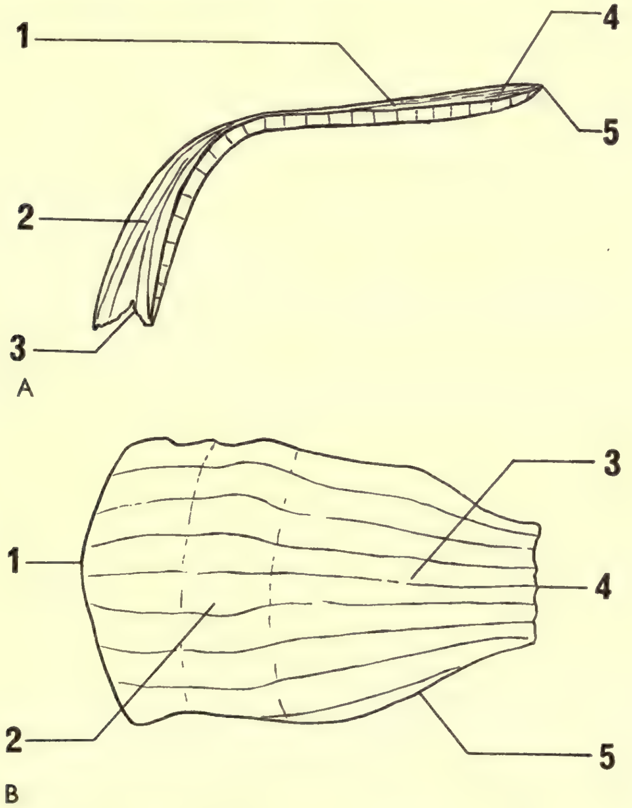
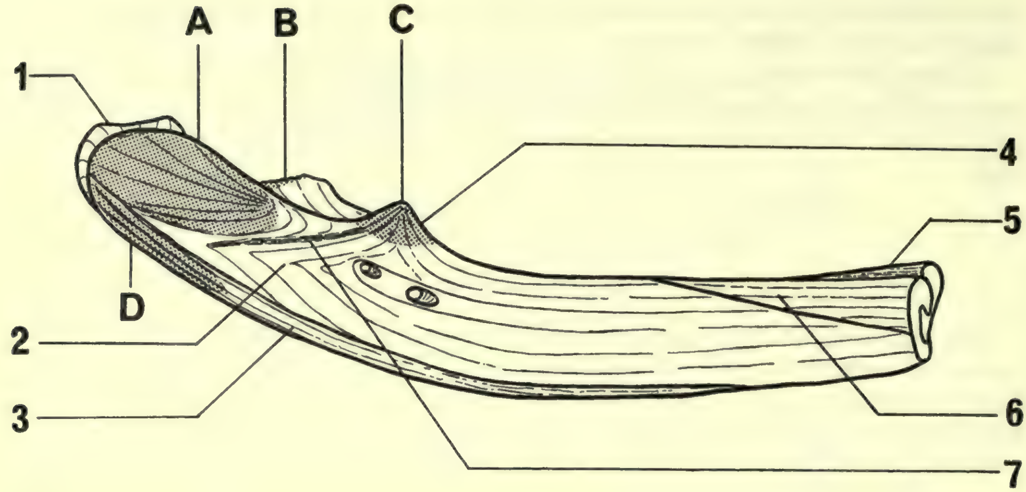


Fig. 24. (a). Sclerotic plate, side view, ×2 (R6697). 1, anterior surface. 2, lateral surface. 3, outer margin. 4, shallow sulcus. 5, inner margin. (b). Sclerotic plate, anterior view, ×2, (R6697). 1, outer margin. 2, lateral surface. 3, anterior surface. 4, inner margin. 5, lateral margin.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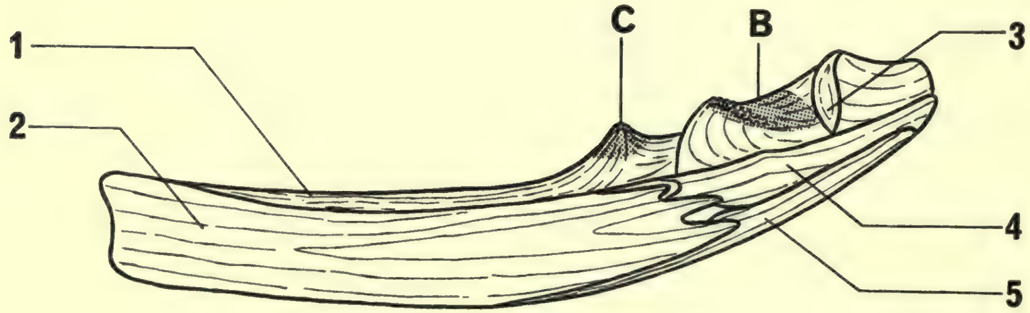
A



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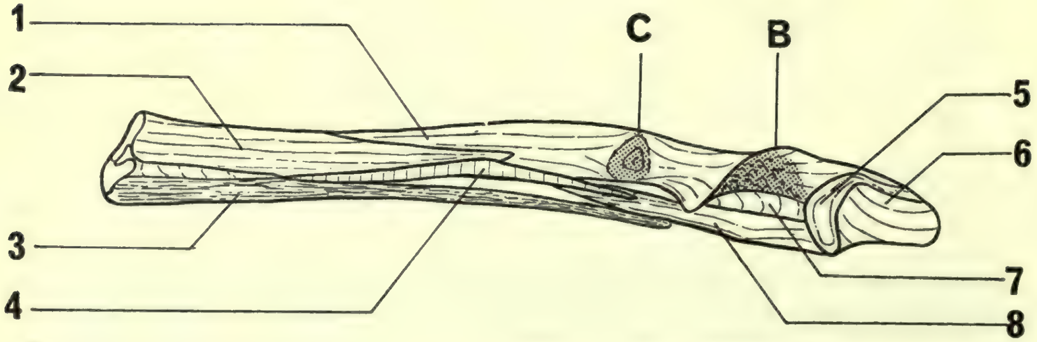
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fore to deal in very much detail with those aspects which have already been satifactorily discussed elsewhere, (the reader is referred in particular to the work of Sollas, 1916, for a very adequate account of the jaw).

The mandibular ramus is formed largely from the surangular, angular, splenial, and dentary. The prearticular makes a minor contribution to the medial jaw surface, while the role of the coronoid in its contribution to the dorsal surface is even smaller.

1. *Surangular* (fig. 25). The surangular forms the greater part of the external surface of the posterior region, and much of the dorsal aspect. Postero-ventrally it bears a deep and tapering recess into which the posterior portion of the angular locates. In the specimen sectioned by Sollas the relationship between these two elements is more intimate, due to interdigitation. Anteriorly the surangular is gradually overlain by the dentary, and therefore has a tapered appearance when viewed from the side. The surangular bears three prominent muscle insertion areas which have not been adequately described elsewhere, and these will now be considered.

Posteriorly and dorsally, on the external surface, there is an ovoid and slightly depressed area marked by numerous striations which tend to converge anteriorly and somewhat ventrally. This is the largest of the mandibular insertions, and, as will be seen later, is identified as that of the *M. depressor mandibulae.* The dorsal margin of the surangular is for the most part rounded from side to side, but the uniformity is interrupted caudally by a bony protuberance which has been described as the coronoid process. The coronoid process is pitted and marked by low rugosities and is interpreted as marking the insertion of the *M. adductor mandibulae pseudotemporalis.* The superficial sculpturing of the bone widens medially so that the area of insertion has a triangular dorsal aspect, the wide base of which lies medial and parallel with the longitudinal axis.

Some small distance behind the coronoid process the internal surface of the surangular is deflected outwards, exposing a demilunar and dorso-medially inclined

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FIG. 25. (a). Lower jaw ramus (right side), external view, slightly more than 1/2 natural size (R8177). (Position of articular and terminal portion of jaw is part restored by reference to R6697 and Evans' nodule.) 1, articular. 2, surangular. 3, angular. 4, coronoid process of surangular. 5, splenial. 6, dentary. 7, raised lip which might have been part of the insertion area of the *M. adductor mandibulae externus.* (A) Insertion of the *M. depressor mandibulae* (the anteriormost portion of this shaded area may well mark the position of insertion of ligaments of the jaw joint capsule). (B) Insertion of the *M. adductor mandibulae externus.* (C) Insertion of the *M. adductor mandibulae internus pseudotemporalis.* (D) Insertion of the *M. adductor mandibulae internus pterygoideus.* (b). Lower jaw ramus (right side), internal view, slightly more than 1/2 natural size (R8177). 1, surangular. 2, splenial. 3, articular surface of articular. 4, prearticular. 5, angular. (B) Insertion of the *M. adductor mandibulae externus.* (C) Insertion of the *M. adductor mandibulae internus pseudotemporalis.* (c). Lower jaw ramus (right), dorsal view, slightly more than 1/2 natural size. 1, surangular. 2, dentary. 3, splenial. 4, coronoid. 5, articular surface of articular. 6, smooth dorso-medial surface of articular. 7, Meckelian fossa. 8, prearticular. (B & C) As for Figure 25 (b).

surface which is prominently roughened and marked by striations which converge antero-ventrally. This area is bounded laterally by the sharp dorsal edge of the surangular, which, curving towards the mid line anteriorly, is produced into a trenchat crest which faces obliquely inwards and forwards. Here the rugosities are most prominent and are dentiform. This very prominent insertion is interpreted as that of the three components of the *M. adductor mandibulae externus.*

The external surface of the surangular is excavated by a short but moderately deep groove which commences at the level of the coronoid process, and about half way down, and which is pierced by two oval foramina. These foramina open out medially into the Meckelian canal, and probably transmitted blood vessels from the Meckelian canal to the external surface of the jaw.

2. *Angular* (fig. 25). The angular contributes to the external surface of the jaw and lies ventral to, and is overlapped by, the surangular. Ventrally the angular is inflected and forms the ventral jaw margin for some distance, and much of the internal jaw surface posterior to the level of the coronoid process. Anteriorly the angular disappears from view beneath the ventral embrace of the splenial, but persists clandestinely for some considerable distance.

The terminal portion of the external surface is marked by a series of longitudinal striations which are interpreted as the insertion of the *M. adductor mandibulae internus pterygoideus.*

3. *Splenial* (fig. 25). The medial surface of the jaw is formed for almost its whole length by the splenial. Anteriorly the ventral splenial edge is outward turned and, embracing the angular from below, forms the ventral margin of the jaw. The splenial terminates posteriorly in a digitate edge just posterior to the level of the coronoid process.

4. *Dentary* (fig. 25). The dentary commences posteriorly, some distance in front of the coronoid process, as a slender splint of bone which is applied to the dorsal edge of the surangular. As the dentary increases in width anteriorly, it spreads over the external surface of the jaw and encroaches upon the surangular which it eventually covers completely. The dorsal margin of the dentary contributes with that of the splenial in the formation of a dentigerous groove.

5. *Prearticular* (fig. 26, plate 6b). The prearticular is a slender laterally compressed element which contributes, posteriorly, to the medial surface of the jaw. Ventrally it is overlapped by the angular and almost half of its depth is hidden from view. The area of contact with the angular is marked by a longitudinal articular facet. In the specimen sectioned by Sollas the prearticular (referred to by Sollas as the goniale) is shown to lie in the same vertical plane as the angular throughout its length. Furthermore it is shown to lie in articular contact with the splenial and in the same vertical plane for some distance (sections 457–462) before being overlapped, whereas in specimen R8177 the splenial always overlaps the prearticular.

The anterior half of the prearticular is quite straight but slightly twisted about a longitudinal axis so that the dorsal edge comes to lie just labial of the ventral edge.

Somewhat more than halfway along from its anterior end the bone is curved slightly inwards, and at this point the direction of torsion is reversed so that the dorsal edge comes to lie just medial of the ventral edge. Caudally the bone is gently upturned so that the entire element has the appearance of a complete jaw ramus when viewed from the side. For most of its length the cross-section is wedge-shaped, tapering gradually ventrally, and the depth and thickness decrease rostrally where the bone ends in a bifid tongue.

Posteriorly and ventrally the medial surface bears the longitudinal angular facet, and the ridge which forms its dorsal border is thickened anteriorly, forming a prominent lip. In advance of this facet the surface is relatively flat and unsculptured, while the external surface is slightly hollowed over most of its length.

The dorsal edge bears a long groove for reception of the coronoid, and this facet is tapered at either end and is inclined labially.

6. *Coronoid* (fig. 27, plate 6c). There has been some confusion in the literature over the use of the term *coronoid*. Conybeare (1821 and 1822) uses it synonymously with *surangular*, while Andrews (1910) uses it to describe the *prearticular*. The true coronoid has hitherto escaped notice in the Ichthyosauria, and full credit for its discovery is due to Rixon whose careful preparation of specimen R8177 revealed the presence of this frail and elusive element.

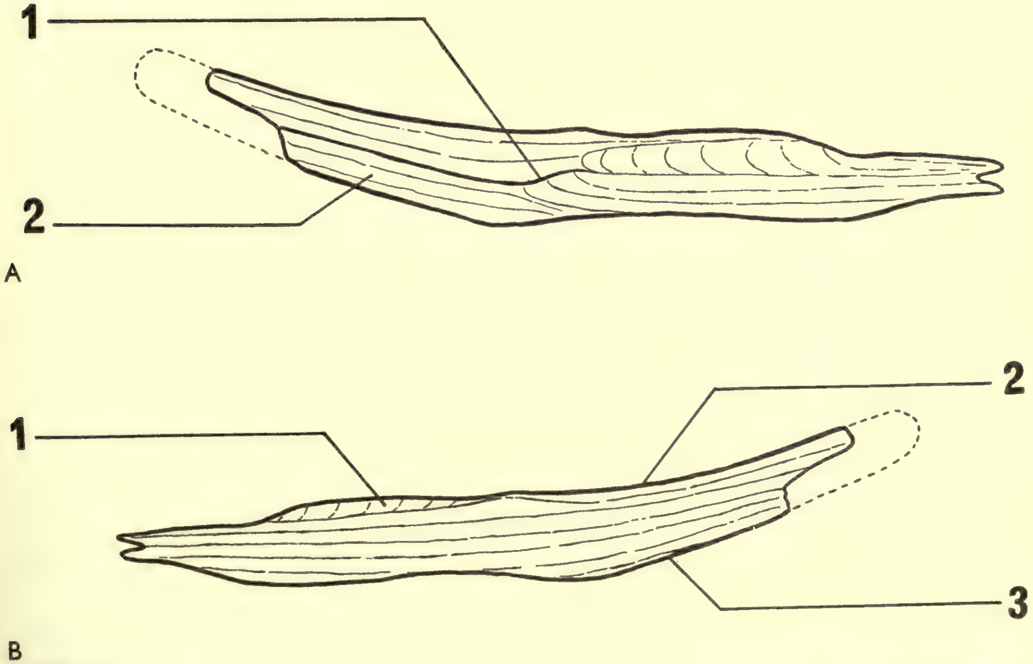

Fig. 26. (a). Prearticular (left), internal view, natural size (R8177). 1, dorsal border of angular facet. 2, angular facet. (b). Prearticular (left), external view, natural size (R8177). 1, coronoid facet. 2, dorsal edge. 3, ventral edge.

The coronoid is a very slender and fusiform element which lies in the dorsal dentigerous groove of the mandible, extending for some distance forward beyond the level of the coronoid process of the surangular. The dorsal surface therefore contributes to the dorsal aspect of the mandible, and it rests with its posterior third in the prearticular groove. In cross section it is triangular and the medial surface lies at right angles to the relatively flat and dorsal surface. The labial surface is therefore oblique and faces downwards and outwards. Viewed from above both internal and external dorsal edges describe arcs about centres which lie medially. Since the radius of curvature of the external edge is less than that of the internal edge, the bone widens towards its centre. The depth of the element is also greatest towards its centre. Because of the arcuation of its dorsal edges the coronoid does not make lateral contact with the rest of the jaw over its entire length. In the mid-portion of the element, where external lateral contact with the surangular and posterior portion of the dentary is made, the ventro-lateral surface bears a shallow articular facet for this purpose.

The widest part of the element is not coincident with its linear centre but lies caudally, so that the anterior process is longer than the posterior process, and is accordingly more slender. The anterior process also differs from the posterior in the possession of two small foramina which pass antero-ventrally through the bone.

7. *Articular* (fig. 28, plate 6d). The articular is a small laterally compressed element, which lies at the posterior end of the jaw ramus with the whole of its rounded external surface applied to the medial surface of the surangular. Ventrally its medial surface bears a triangular articular facet for the prearticular. This orientation

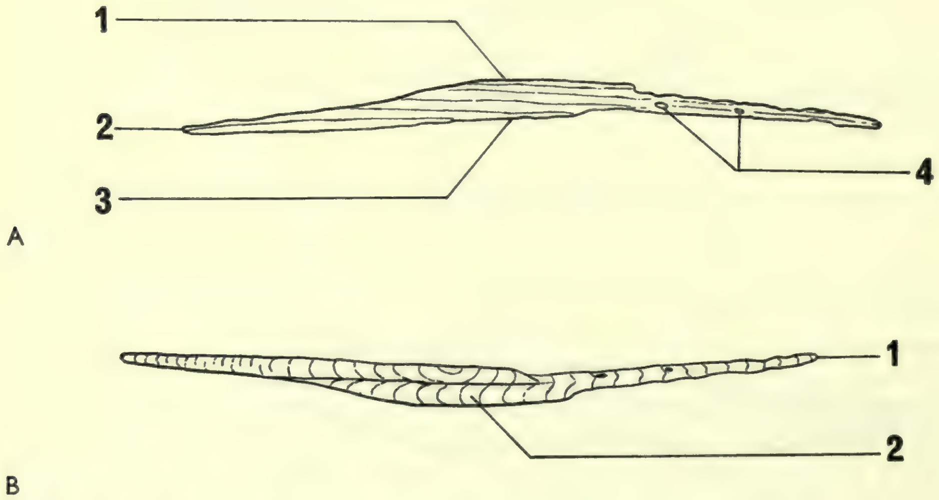

FIG. 27. (a). Coronoid (left), dorsal view, natural size (R8177). 1, external edge. 2, posterior end. 3, internal edge. 4, foramina. (b). Coronoid, (left), ventral and somewhat external view, natural size (R8177). 1, anterior tip. 2, articular facet for surangular and dentary.

has been unequivocally established, and, as will be seen later, gave rise to some difficulties in obtaining a satisfactory relationship with the quadrate.

The external surface is roughened and somewhat depressed, and has an oval outline, whereas the internal surface, is relatively smooth and almost rectangular in outline. From before to behind this surface is concave, while from top to bottom it is convex, conferring a superficial resemblance to a saddle.

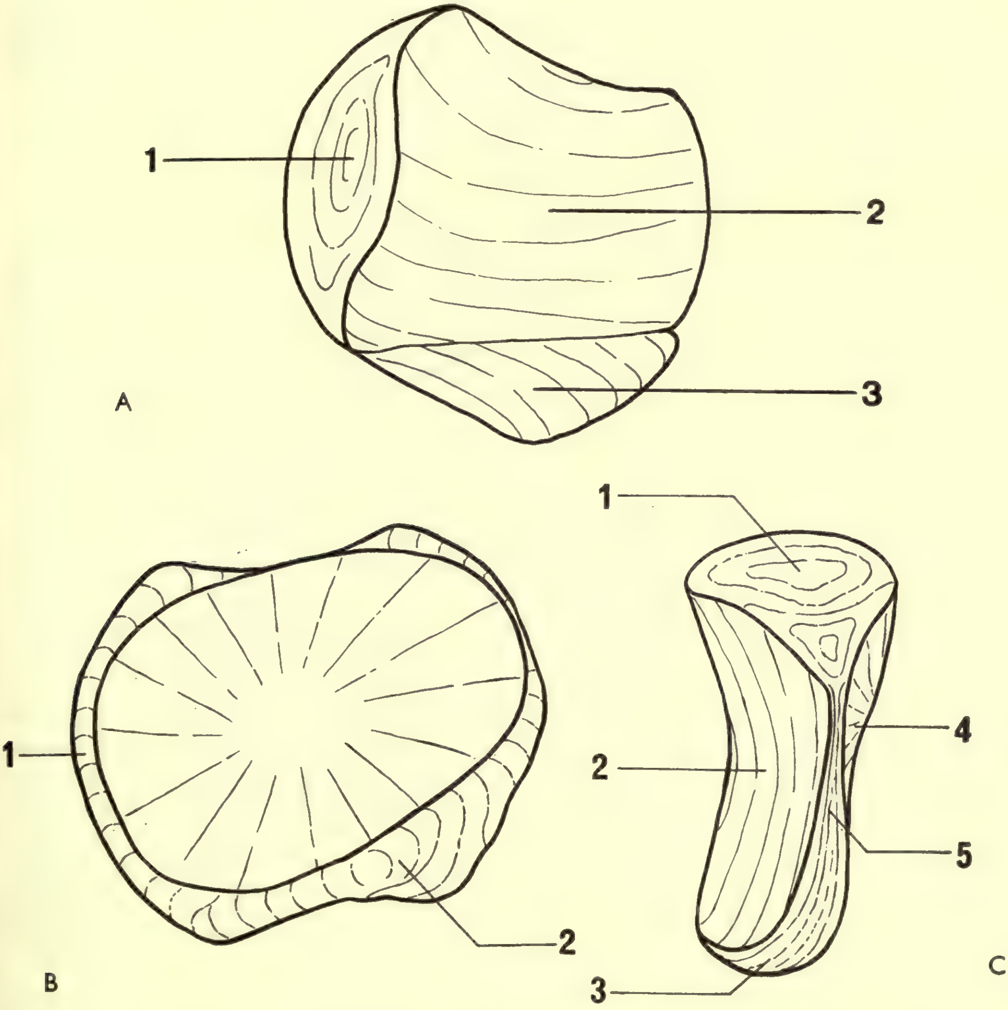

Fig. 28. (a). Articular (right), lingual view, ×3 (R6697). 1, articular surface. 2, medial surface. 3, prearticular facet. (b). Articular (right), labial view, ×3 (R6697). 1, posterior margin. 2, ventral surface. (c). Articular (right), dorsal view, ×3 (R6697). 1, articular surface. 2, medial surface. 3, posterior margin. 4, external surface. 5, dorsal surface.

The articular is thinnest somewhere about its centre, and, thickening rapidly anteriorly, reaches its maximum thickness at its anterior face which has a relatively smooth surface, and is ellipsoid when viewed from in front. The posterior margin is relatively smooth and is narrow.

The ventral surface is narrow and triangulate, tapering caudally, and is coarsely corrugate. The dorsal surface is virtually non-existent, being the labially inclined dorsal portion of the internal surface.

In two specimens (R8177 and 49203) the articular has been preserved in approximately its natural position, and this provided the initial clue to its correct orientation. The articular lies with its rugose external surface firmly braced against the internal surface of the surangular, and the posterior edge faithfully follows the curvature of the surangular margin. Meso-ventrally contact with the prearticular is made in a well defined facet.

THE JAW ARTICULATION

The orientation of the quadrate, like that of the articular, has been established beyond all reasonable doubt, and the problem of the jaw articulation is that of determining their correct relationship with one another. Initially it was thought that the ventral surface of the quadrate condyle articulated with the saddle-shaped medial surface of the articular. However the only satisfactory relationship between these two surfaces could be obtained with the jaw in the vertical plane, at right angles to the longitudinal axis of the skull. Furthermore the medial surface of the articular is quite smooth and does not have the appearance of bone once invested in cartilage. The anterior surface of the articular, however, does have such an appearance, and when articulated with the postero-laterally inclined portion of the quadrate condyle a satisfactory relationship is obtained, their undulating surfaces corresponding moderately well (fig. 29). Thus oriented the articular lies entirely posterior to the level of the jaw joint and there is therefore a significant retroarticular process. The most convicing evidence that this is the correct relationship between the jaw and skull is furnished by two associated skulls, 49203 and R3375. The first is a complete in-the-round specimen, and from the way in which the upper and lower teeth mesh throughout, it is clear that the jaw is in its correct relationship with the skull. The quadrate condyle and the articular are both clearly visible on the right side, and the latter lies entirely posterior to the level of the former. In R3375, which has been dorso-ventrally compressed, only the dorsal half of the skull is exposed and it cannot be known for sure whether the jaw is in its correct position, but this does seem to be the case. Here again quadrate condyle and articular are clearly visible and the articular lies posterior to the quadrate.

THE HYOID APPARATUS

(fig. 30)

The hyoid arch is represented by a pair of stout rods which lie medial to, and parallel with, the jaw rami. These rods are gently curved, and extend from about

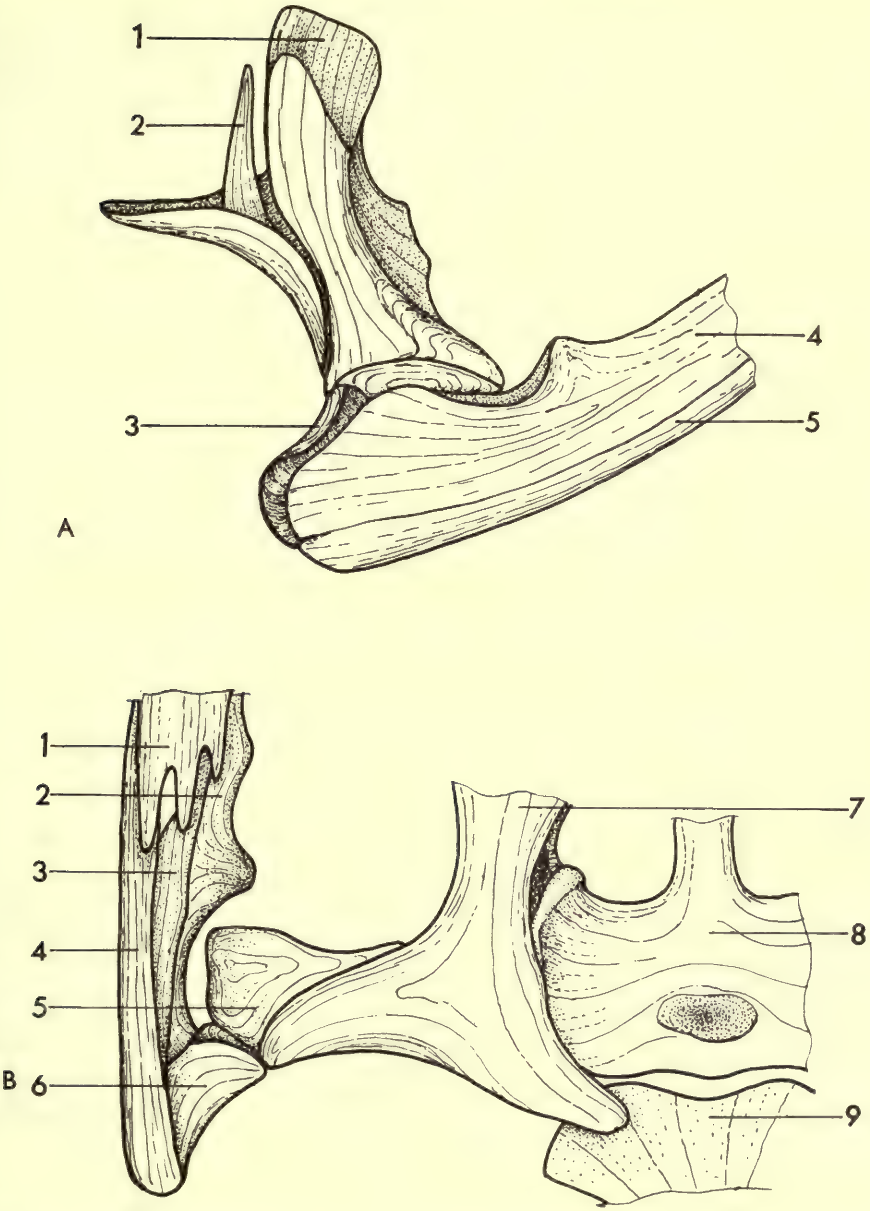

FIG. 29. (a). A reconstruction of the jaw joint (right side), postero-lateral view. 1, quadrate. 2, quadrate wing of pterygoid. 3, dorso-medial surface of articular. 4, surangular. 5, angular. (b). Reconstruction of the jaw joint (right side), ventral view. (In order to demonstrate the jaw joint more clearly the jaw has been rotated outwards somewhat and is shown in a ventro-lateral aspect.) 1, splenial. 2, surangular. 3, prearticular. 4, angular. 5, condyle of quadrate. 6, ventro-medial surface of articular. 7, pterygoid. 8, basisphenoid. 9, basioccipital.

the level of the quadrates almost as far as the anterior border of the orbit. They are often preserved in dorso-ventrally compressed specimens, and are figured by Owen, (1881, pl. 25, fig. 3). Sollas gives a very good account of the hyoid skeleton and also describes the elements of the first branchial arch, which, together with those of the hyoid, form a complex ventral skeleton (Sollas 1916, fig. 2, sections 425–507; fig. 15). For completeness Sollas' reconstruction of the hyoid and branchial skeleton is given below (fig. 30).

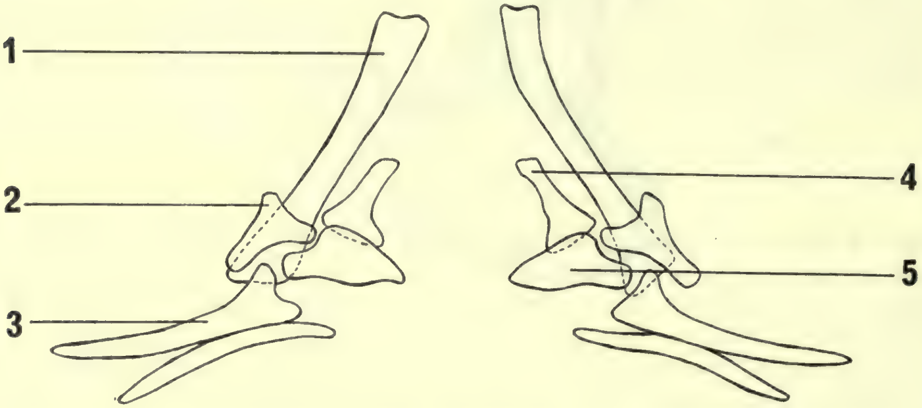

FIG. 30. Hyoid apparatus (ventral view), after Sollas. 1, hyoid rod. 2, first branchial arch. 3, second branchial arch. 4 & 5, third branchial arch.

THE TEETH

The teeth are somewhat variable in shape but generally have the form of fairly stout and curved cones. The crown, which has an enamel coating, forms but a small portion of the tooth, and though smoother than the root, it usually bears fine striations. The root is rough to the touch, is distinctly corrugate towards its base, and has a porous texture. The junction between the root and crown is marked by a raised annulation which may be smooth or ridged (fig. 31, plate 6g). The teeth have been very adequately figured and described by Fraas (1891 : pl. 1–2) who includes some excellent figures of sections.

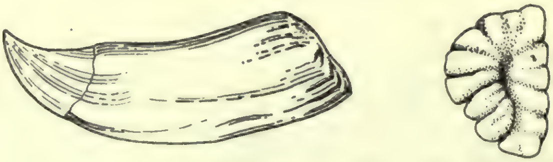

FIG. 31. Tooth from 49203, × 2 1/2.

THE RECONSTRUCTION OF THE SKULL

The skull reconstruction was carried out almost entirely with reference to ex-nodular material, and since the snout region is unrepresented there, the relevant information has been obtained by studying unprepared skulls, part-prepared skulls and sections. (The work of Sollas 1916 has been particularly useful.)

Sufficient material was available to permit the reconstruction of three hind skulls, and these were built up in parallel so that comparisons could be made between them at each stage, thus reducing the possibility of misinterpretation. Before commencing the reconstructions, however, it was necessary to take each bone and orientate it with respect to its adjacent elements until the precise relationship of each bone had been established, and recorded upon the bones themselves using keying-up marks. The three skulls were then reconstructed, fixing together component elements with water-soluble wax. In only one of the specimens, R8177, was it possible to reconstruct the skull roof and palate up to the external narial opening, though at least part of the temporal vacuity and parietal roof and part of the palate could be reconstructed in the other two specimens. Since the reconstruction proceeded in a number of distinct stages, the following account is subdivided.

1. *The reconstruction of the occiput* (fig. 32, plates 7b and 7c)

The occiput comprises the single median basioccipital, basisphenoid, and supraoccipital, and the paired exoccipitals, opisthotics, pröotics, and the stapes. The first elements to be articulated were the basioccipital and basisphenoid, the foundation stones of the skull.

The postero-dorsal surface of the basisphenoid is deeply grooved for the reception of the keeled antero-ventral surface of the basioccipital, and it was found that the two elements fitted together with only a small degree of freedom enabling a good relationship to be obtained. As noted earlier when the structures of the basisphenoid and basioccipital were described, the small notch which lies just ventral on the basioccipital peg corresponds with the dorsal fissure of the basisphenoid marking between them the position of the upturned tip of the notochord. This relationship enables a very precise orientation to be made between the two elements. Since the basioccipital keel does not make flush mid-line contact with the deep basisphenoid groove a narrow channel is formed. This channel opens dorsally into the notochordal recess, and ventrally into a large eliptical aperture enclosed by the ventral edges of the two elements. This median ventral aperture corresponds closely in its position with the single Eustachian aperture of the crocodile, a fact which did not escape the attention of Owen (1881, 93) who wrote, "The fore part of the basioccipital presents, in some species, a slight notch or groove, as if for the outlet of an Eustachian canal." However, since the channel opens proximally into the cranial cavity it is inconceivable that it served an otic function and it seems most likely that it has no significance at all, merely arising out of the loss of mid-line contact between the basioccipital and basisphenoid. Indeed, since the channel is so narrow it is doubtful whether it did exist in life, being occluded by cartilage or periosteal membranes. In orientating the basisphenoid and the basioccipital, care

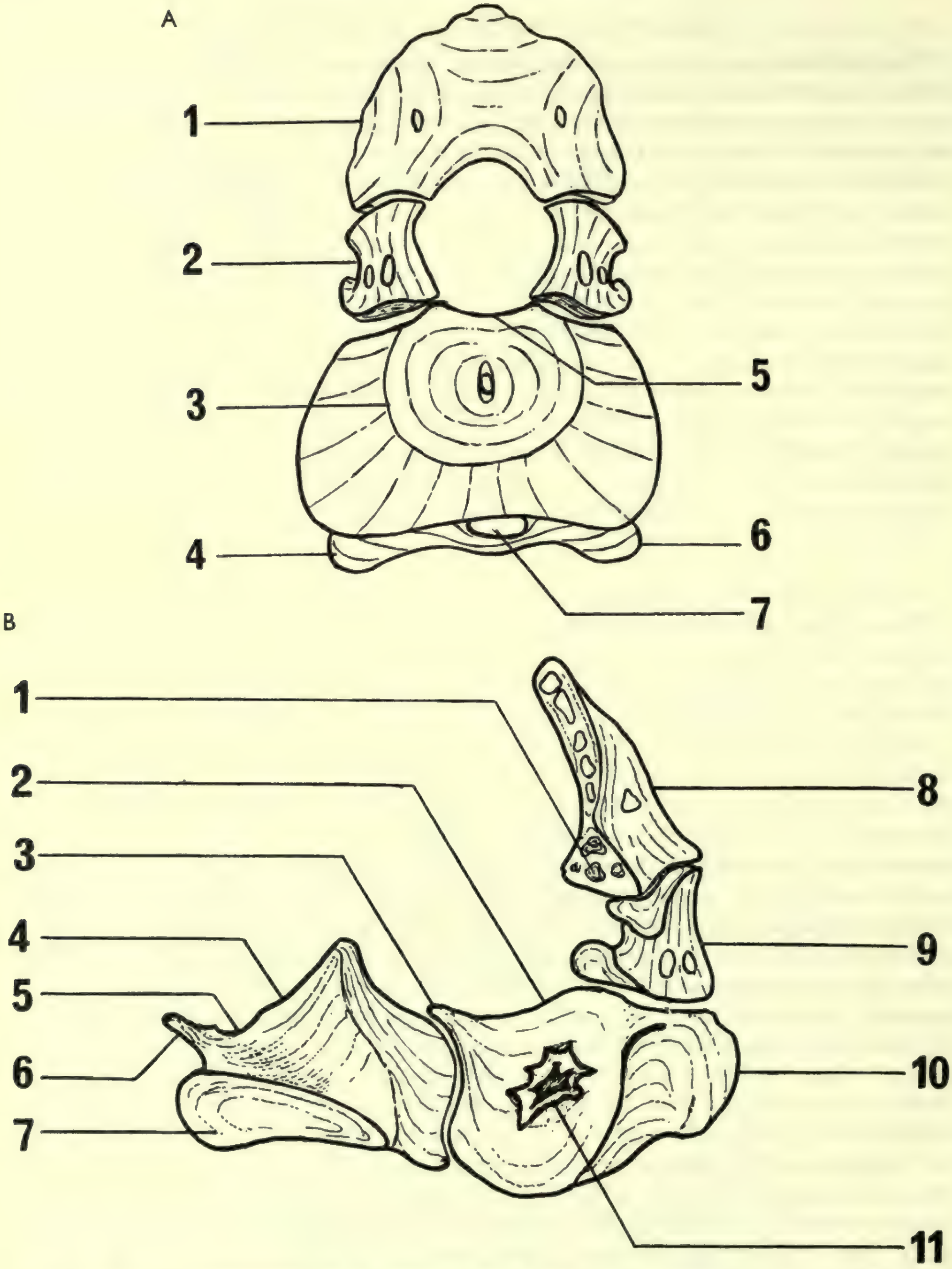

FIG. 32. (a). Reconstruction of occipital region of skull, posterior view, × 1 (Evans' nodule). 1, supraoccipital. 2, exoccipital. 3, basioccipital condyle. 4, basisphenoid. 5, floor of foramen magnum. 6, basipterygoid process. 7, carotid foramen. (b). Reconstruction of occipital region of skull, lateral view, × 1 (Evans' nodule). 1, membranous impression. 2, ascending dorsal surface of, × 1. 3, basioccipital peg. 4, position of sella turcica. 5, position of paired trabeculae impressions. 6, parasphenoid. 7, basipterygoid process. 8, supraoccipital. 9, Exoccipital. 10, basioccipital condyle. 11, stellate excavation of basioccipital.

was taken to ensure that they laid symmetrically about a longitudinal axis, and, having obtained a satisfactory relationship, attention was turned to the supraoccipital and paired exoccipitals.[1]

The articular facets for reception of the exoccipitals on the supraoccipital are deep and well defined, and it was found that the medial portion of the dorsal articular surface of the exoccipital located with precision, so that there was neither discontinuity in the cranial wall when viewed from within, or in the curvature of the foramen magnum when viewed from behind. The exoccipitals could thus be attached to the supraoccipital very accurately. The supraoccipital with its attached exoccipitals was lowered into position on the basioccipital. It was found that the exoccipitals fitted into the facets on the basioccipital so that the continuity of the foramen magnum was uninterrupted, and the medial ventral edge of each followed the contour of the basioccipital facet exactly. The paired exoccipital facets of the basioccipital are fairly shallow, and less well defined than those of the supraoccipital, and a flush contact between the respective articular surfaces does not occur at every point, indicating the intervention of a thin layer of cartilage between them (fig. 32).

Since the occipital elements fitted together so precisely it could confidently be concluded that the reconstruction was accurate. Before the otic elements could be oriented, however, it was necessary to reconstruct the rest of the skull and relate it to the occiput. The next stage was the reconstruction of the palate and the determination of its relationship with the rest of the skull.

2. *The reconstruction of the palate, and its relationship with the rest of the skull* (fig. 33, plate 7a)

The palate comprises of paired pterygoids, palatines, and vomers, and the median parasphenoid. The two halves of the palate form extensive shelves of bone which, narrowing rapidly, come into contact just anterior to the level of the internal nares. Posterior to this level the palate is formed largely from the pterygoids and palatines, and the vomers, which contribute with the palatines in the formation of the internal narial aperture, make but a minor contribution. Anterior to the nares the palate is formed entirely from the vomers, although the pterygoids do continue for some distance hidden from view.

The pterygoid and palatine were the first elements to be associated, and they were shown to have a very precise relationship with one another. Fusion does not seem to have occurred, except perhaps at the medial margin of the palatine, strength having been attained by overlapping. The palatine overlaps the pterygoid dorsally, and not ventrally, as figured by Owen (1881 : pl. 25, fig. 1). The posterior margin of the palatine slopes obliquely backwards towards the midline so that when placed in contact with the outer edge of the pterygoid the curvature of the intrapterygoid vacuity is continued without interruption (fig. 33, plate 7a). Furthermore, there is a small ovoid facet on the dorsal surface of the pterygoid, at the anterior corner of the intrapterygoid vacuity, which articulates with a corresponding facet on the posterior ventral surface of the palatine. Anteriorly there is a third point of reference, provided by a raised bony ridge on the dorsal surface of the pterygoid, against which abuts part of the internal palatine margin. Since both the palatine and pterygoid are curved from side to side, they form a basin when placed together.

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[1] In R8177 the exoccipitals are not preserved, but the problem was overcome by making a pair of plaster elements to scale, by reference to the small skulls.

The pterygoid narrows rostrally, and, due to torsion, the surface which posteriorly was dorsal, becomes turned outwards, forming an almost vertical surface which has articular contact with the medial surface of the vomerine keel. The latter surface bears a low longitudinal ridge which corresponds with a shallow groove in the pterygoid. Viewed from beneath, the outer edge of the pterygoid slopes gently forward towards the midline, and the keel of the vomer faithfully follows this line. Dorsally the vomer overlies the anterior portion of the pterygoid, obscuring it from

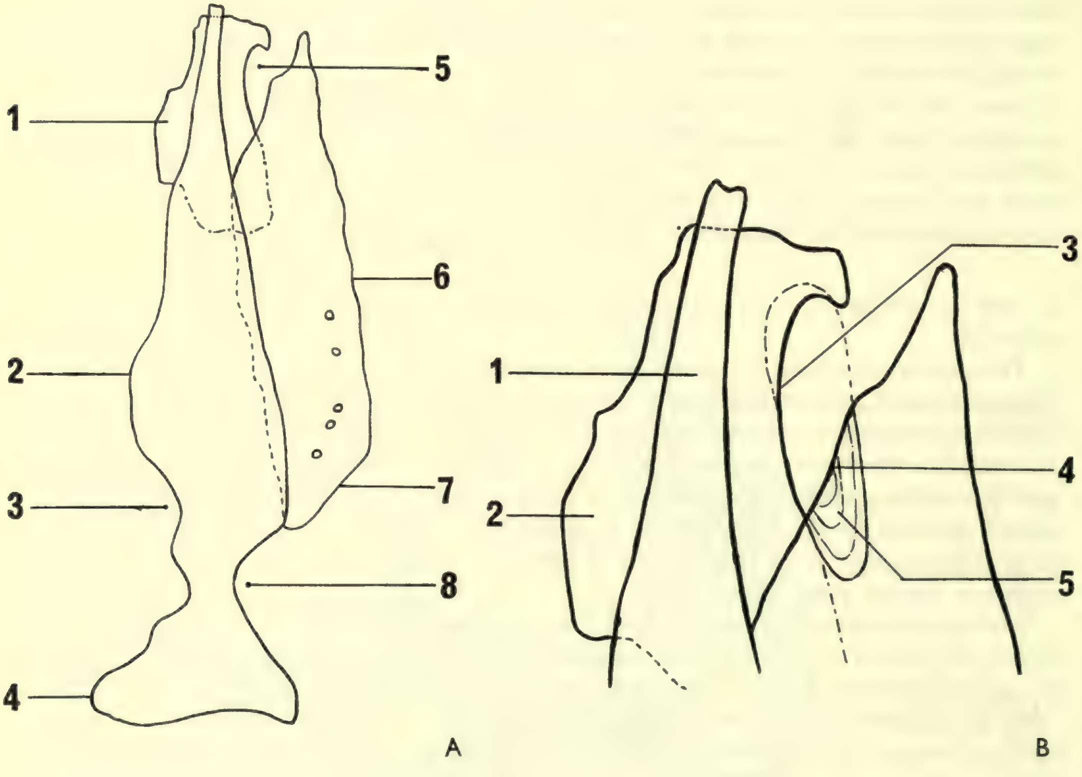

FIG. 33. (a). Reconstruction of palate (left side), ventral view, ×1/2 (R8177). 1, vomer. 2, medial edge of pterygoid. 3, edge of interpterygoid vacuity. 4, medial wing of pterygoid. 5, internal narial aperture. 6, external edge of palatine. 7, posterior margin of palatine. 8, intrapterygoid vacuity. Note: Palatine lies dorsal to pterygoid and vomer lies dorsal to palatine. (b). Reconstruction of the internal narial aperture (left side), ventral view, slightly greater than natural size (R8177). 1, pterygoid. 2, vomer. 3, external edge of vomer. 4, medial edge of palatine. 5, depression.

dorsal view, (see Sollas 1916 : sections 334–359). Furthermore, since the pterygoids tend to curve upward toward their tip, and the vomers meet in midline beneath them, the pterygoids disappear from ventral view. An excavation of the outer edge of the vomer and of the medial edge of the palatine together form the internal narial aperture (fig. 33).

The parasphenoid is present in only one specimen, and is very incomplete, being represented for only a fraction of its entire length. As described above, the parasphenoid is fused with the basisphenoid so that its relationship with the rest of the palate could only be established after attachment of the palate to the occiput.

The relationship between the palate and occiput The only contact between the occiput and the palate is at the basisphenoid, which is drawn out on either side into the winged basipterygoid processes which slot into a deep recess in the pterygoids. The basipterygoid joint is quite definite, but possesses a certain degree of freedom, and two criteria have been used in arriving at a satisfactory relationship.

1. The distal facet of the basipterygoid process is smooth and flat and faces outwards and upwards, and corresponds with an oblique medial facet in the pterygoid slot.

2. The curved edge of the internal pterygoid emargination is continued by the rounded leading ventral edge of the basisphenoid.

These criteria, however, do not unequivocably fix the position of the two halves of the palate, and since the palate has contact with the rest of the skull at three other points, it was necessary to reconstruct much of the skull before the true relationships of the palate could be established. These three points of contact are listed below.

1. With the quadrate, which in turn has contact with the temporal arcade.

2. With the maxilla which has contact with the circumorbital series and with the premaxilla.

3. With the epipterygoids which in turn articulate with the skull roof.

The relationship between the palate and quadrate. The relationship between the quadrate and palate can readily be obtained because the quadrate has a precise contact with the pterygoid over a relatively large area. The postero-lateral surface of the quadrate is somewhat convex, and the quadrate process of the pterygoid is hollowed to receive it in a fairly flush contact. The rounded ventral edge of the quadrate process conforms very closely to the curved edge of the quadrate, and the leading ventral edge of the quadrate fits into a shallow groove located just posterior and external to the epipterygoid groove, and continues the curvature of the intrapterygoid vacuity without interruption.

The relationship between the palate and maxilla. Anteriorly, and towards its external edge, the ventral surface of the palatine is carinate and the depth and width of this keel diminishes posteriorly. The dorsal surface of the maxilla possesses many grooves and medially is a shallow groove which faces inwards and slightly upwards, narrowing posteriorly. The outer surface of the palatine keel locates in this groove and there is a pair of apertures towards the medial margin of the maxilla which corresponds with a pair of emarginations of the outer edge of the palatine. The two elements can be articulated with a good degree of accuracy. The apertures doubtlessly served for the transmission of blood vessels or nerves, and movement between the two elements could not have taken place, (see *Kinesis*, below).

Any further discussion of the palate will be postponed until the reconstruction of the rest of the skull has been dealt with.

3. *The reconstruction of the posterior skull roof and temporal vacuity*

The posterior skull roof comprises of paired parietals, frontals and nasals. Anteriorly the nasals are overlapped by the paired premaxillae which form the major part of the elongate snout. Laterally the nasals, frontals, and parietals have contact with the dorsal components of the circumorbital series. The pre- and post-frontals and the parietals have postero-lateral contact with the paired squamosals.

As mentioned above, the parietals come together in mid-dorsal line in a complex suture, but their union was not found to be without a degree of mobility, for the parietals could be rocked upon one another about an axis passing through the suture. They could therefore be articulated either with the dorsal edges of their sutural

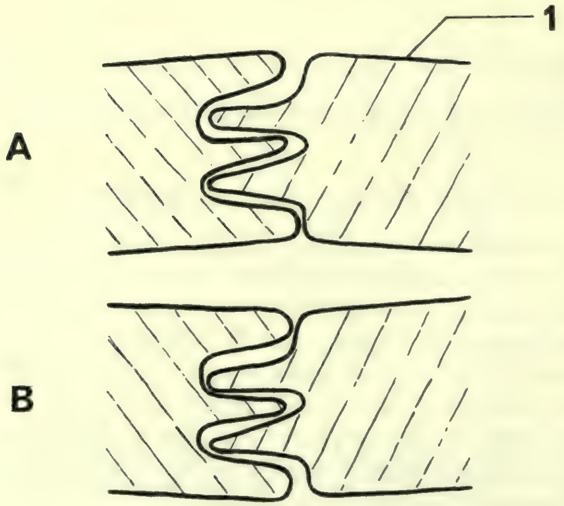

FIG. 34. Transverse section through the parietal suture. (A) Parietals articulated with their ventral edges in contact. (B) Parietals articulated with their dorsal edges in contact. 1, dorsal surface of parietal.

surfaces in contact, or, at the other extreme, with their ventral edges touching, (fig. 34). Whereas the dorsal edges are relatively straight, the ventral edges are jagged and correspond throughout their length, and the most satisfactory relationship seemed to be obtained when these ventral edges were placed into contact. With the parietals thus united their dorsal contact edges were widely separated, but it seemed reasonable that this gap would have been filled with cartilage in life. The relationship could be examined by attaching the epipterygoids and seeing if the distance between their distal facets approximated to the distance between the groove upon the pterygoids for their reception.

The relationship between the parietals and epipterygoids. The epipterygoid has an intimate relationship with the parietal, and the two elements can be articulated with precision. Dorsally the shaft of the epipterygoid is expanded forming a flange which locates in a shallow depression on the internal surface of the epipterygoid process of the parietal. A little further down this process enters into an oblique and interdigitating suture with the fluted external surface of the epipterygoid shaft, forming a rigid union. The epipterygoid could thus accurately be attached to the parietal.

Having attached both epipterygoids to the parietal canopy they were lowered into position upon the palate, but it was found that there was not a sufficient separation between them to permit location in the epipterygoid grooves. It was therefore necessary to adjust the parietal union until a satisfactory condition was reached, and this was found to be intermediate between the two extreme positions shown in fig. 34. When a satisfactory union between the parietals had been obtained the posterior skull roof could be completed.

The completion of the posterior skull roof (fig. 35, plate 8a). The leading edges of the parietals are raked so that rostrally they enclose a large V-shaped notch which is grooved for the reception of the posterior edges of the frontals, and a good relationship was obtained. Posteriorly the medial edge of each frontal is emarginated so that between them they enclose the pineal foramen. For the remainder the medial edges are straight, though down-curved due to the curvature of the element, and meet in mid-dorsal line in a flush contact. In only one specimen (R8177) are frontals and parietals complete, and there can be no doubt that in this instance the pineal foramen is formed entirely from the frontals with no parietal contribution. Skulls are often figured showing parietal participation in the pineal foramen, and this does not seem unreasonable. Anteriorly the frontals are overlapped for their greater part by the nasals.

On the ventral surface of each nasal is a curved ridge of bone which terminates towards the median line in a low projection which points obliquely backwards. The anterior edge of each frontal approximately corresponds with this ridge, and is embraced from below by the bony projection, so that the relationship between the nasals and the rest of the roofing bones can be accurately established. For the most part the medial edges of the nasals are in contact but at about the level of the anterior edge of the frontals they are slightly emarginated, and enclose between them an elongate foramen, the internasal foramen. Medial contact is resumed once more in front of the foramen in a suture somewhat similar to that uniting the parietals, although far less complex. Posteriorly the nasals widen, and since their lateral and medial edges are somewhat raised, contact with the underlying frontals is made at only one point.

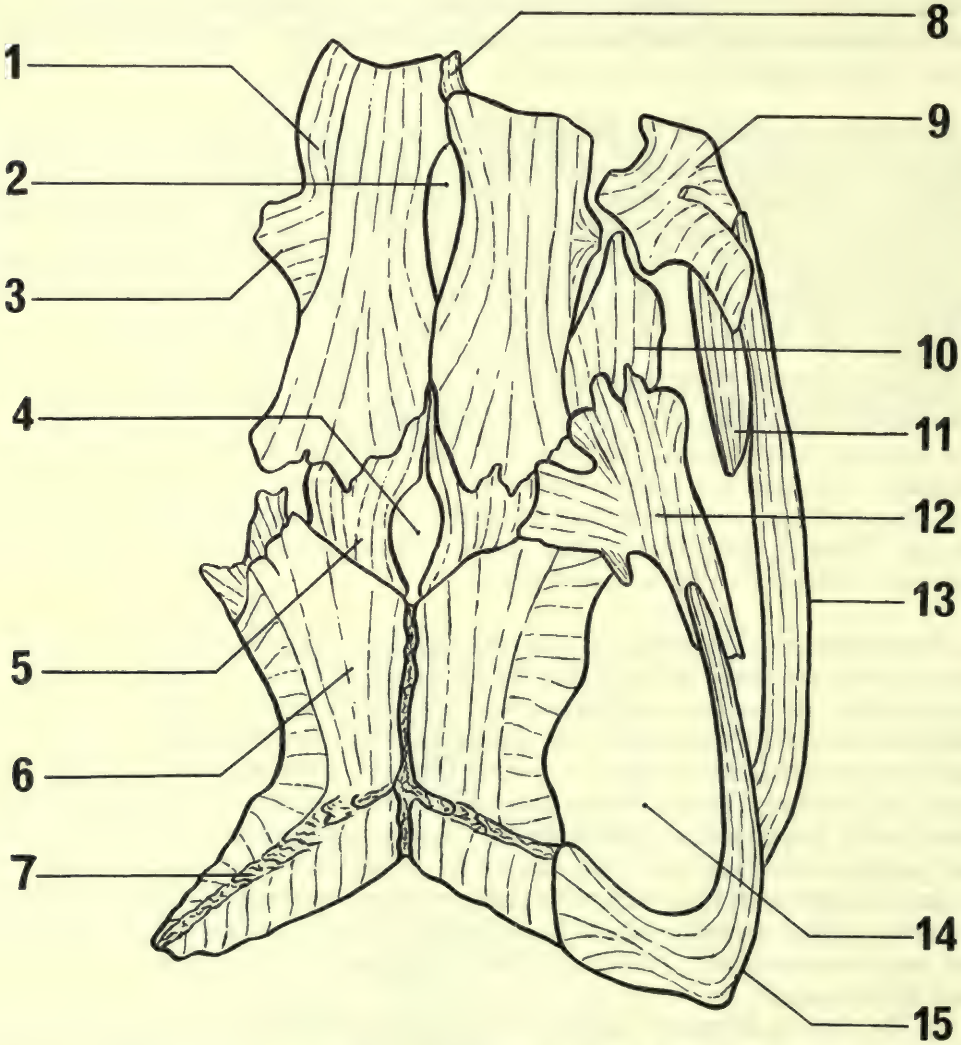

FIG. 35. Reconstruction of the skull roof (and circumorbital series), dorsal view, × 2/3 (R8177). 1, lateral surface of left nasal. 2, internasal foramen. 3, descending triangular process of nasal. 4, pineal foramen. 5, frontal. 6, dorsal surface of parietal. 7, parietal ridge. 8, nasal facet excavated in medial margin of left nasal. 9, lachrymal. 10, prefrontal. 11, maxilla. 12, postfrontal. 13, jugal. 14, temporal vacuity. 15, squamosal.

The prefrontal is an element of the circumorbital series, but since it contributes to the skull roof it will be discussed here. The outer margin of the prefrontal has a smooth surface and contributes to the orbit, whilst medially it is drawn out into a narrow and roughened flange which is overlapped dorsally by the nasal. Ventrally, at its postero-medial corner it is underlapped by the parietal. Anteriorly the roughened medial flange is directed vertically as an ascending shelf of bone which makes contact internally with a descending process from the nasal.

The parietal makes a major contribution to the margin of the temporal vacuity, and the next stage in the reconstruction was the completion of the vacuity.

The completion of the temporal vacuity (fig. 35, plate 8a). The margin of the temporal vacuity is formed internally by the parietal, antero-laterally by the postfrontal, and is completed laterally and posteriorly by the squamosal. That there is squamosal and not supratemporal participation, as was previously supposed, is a matter of much taxonomic importance, and warrants closer examination.

In all the material so far examined there appears to be a single element forming the posterior margin of the temporal vacuity, whereas many other authors have figured and described two; Lydekker 1889 : fig. 2; von Huene 1922 : pl. 15, fig. 1; pl. 16, fig. 35; pl. 18, fig. 1; pl. 19, fig. 1; Watson 1914 : 95. When the temporal region of the reconstructed skulls are examined there is not found to be sufficient space to accommodate a second element, and, if there were one it would have to be ventral and medial to the other in its position, and considerably smaller. It is not altogether inconceivable that a second and very much smaller temporal element did exist and that it has always been lost, but it does seem rather unlikely. In those reptiles possessing both squamosal and supratemporal it is observed that the former is never subordinate in size to the latter, and if both elements existed in the Ichthyosauria, that bordering the vacuity, on *a priori* grounds, would be the squamosal and not the supratemporal. Romer (1968) reached the same conclusion and credits the present author for independently solving the problem.

The squamosal is a large element with two lateral and horizontal rami which embrace the vacuity, and a descending process which has contact with the quadrate (fig. 13, plate 6f). The free ventral margin of the medial ramus carries a deep and ellipsoidal depression which caps the distal portion of the oblique parietal ridge in a union which firmly anchors the squamosal to the parietal.

The postfrontal does not enter into such a definite union with the skull roof, but has an overlapping relationship which appears to be rather imprecise. Antero-medially the postfrontal is drawn out into a flat bony process which has a roughened ventral surface and which is applied to the dorsal surface of the prefontal and parietal. Posteriorly, however, the postfrontal enters into a very precise union with the squamosal. The lateral ramus of the squamosal tapers to a rounded point and the postfrontal bears a dorsal groove for its reception, (fig. 15a). The lateral margin of the temporal vacuity, formed posteriorly by the lateral ramus of the squamosal, is thus continued without interruption by the postfrontal.

The descending process of the squamosal bifurcates into two spatulate flanges of bone which lie in the same plane, and which are set at an oblique angle to the longitudinal axis of the skull. The leading and external edge of the anterior flange is grooved along its entire length, and this groove opens out dorsally into a prominent and horizontal recess. The leading edge of the quadrate slots into this vertical groove, and its dorsal edge locates in the horizontal recess.

It has been noted above that the true position of the two halves of the palate could not be ascertained until the skull reconstruction had been completed, and all that remains now is the completion of the circumorbital series. The stapes and otic elements must also be oriented, but these have no bearing on the relationships of the palate.

4. *The reconstruction of the circumorbital series, and the relationships of the quadratojugal* (figs 36 and 37, plate 7e)

The orbit is formed by the pre- and postfrontals dorsally, the lachrymal anteriorly, the jugal ventrally, and the postorbital posteriorly. The maxilla also participates,

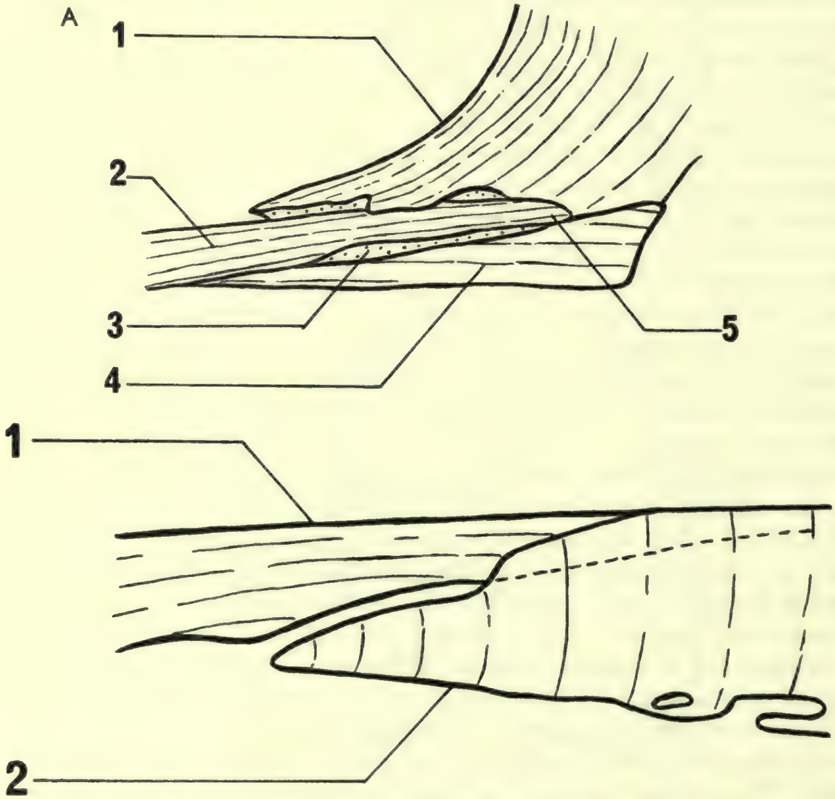

FIG. 36. (a). Antero-ventral corner of the orbit showing the relationship between the jugal, lachrymal and maxilla. External lateral view. 1, orbital margin of lachrymal. 2, jugal. 3, groove in maxilla for reception of the jugal. 4, external surface of maxilla. 5, anterior tip of jugal. (b). Antero-ventral corner of the orbit showing the relationship between the jugal, lachrymal and maxilla. Ventral view. 1, external margin of jugal. 2, medial margin of maxilla.

at its place of union with the jugal and lachrymal, but its contribution is very minor. The pre- and postfrontals are firmly united with the skull roof, the lachrymal is braced against the upper jaw margin, and the postorbital is braced against the quadrate through the quadratojugal.

The relationship between the lachrymal and the prefrontal cannot be known with absolute certainty because there is a degree of distortion in this region, and because it is not altogether clear whether the lachrymal isl compete; the prefrontal is certainly incomplete. The lachrymal is an L-shaped bone whose inner margin is quite smooth and rounded, forming the anterior corner of the orbit. Anteriorly, and also ventrally, the thickness of the bone diminishes and two plates of bone are formed, one vertical the other horizontal. Dorsally the vertical plate overlaps a descending arm of the prefontal, and the tessellate margin of the lachrymal interdigitates with the rugosities of its external surface. The circumorbital margins of the lachrymal and prefontal meet in an oblique union which increases their area of contact giving greater strength. Ventrally the lachrymal enters into a complex union with the maxilla and jugal (Fig. 36a).

The dorsal surface of the maxilla is much fluted, with one particularly prominent bony lamella, which, diminishing in height posteriorly, is reduced to a low ridge. The ventral plate or keel of the lachrymal rests in the outermost groove of the dorsal maxillary surface, braced medially against the bony lamella. This lamella is S-shaped when viewed from above and the internal surface of the lachrymal follows its contours closely. Continuous with this same groove is a deep excavation which receives the anterior portion of the jugal. The lachrymal participates in the jugal articulation, for midway along its external ventral surface it bears a shallow depression for reception of the tip of the jugal, and posteriorly there is a ridge which forms the dorsal border of the maxillary groove. The anterior portion of the jugal has a triangular cross section, the apex being directed medially, and this internal surface is scored by longitudinal striae, and its contours conform closely with the maxillary excavation into which it fits. The jaw margin of the jugal meets the maxilla in an oblique union, (fig. 36b). Posteriorly the jugal articulates with the postorbital and appears also to have contact with the quadratojugal, though poor preservation makes interpretation a little difficult in this region.

The postorbital is a crescentic and laterally compressed element which is divided into two lamellae by a narrow but deep fissure which, commencing fairly high on the posterior margin, somewhat medially, traces a downward curving path to the ventral margin (fig. 16, plate 4a). Into the ventral portion of this fissure, where it is widest, slots the raised and tapered dorsal margin of the terminal portion of the jugal. The sharp leading edge of the quadratojugal slots into the posterior portion. Slotting greatly increases the area of contact conferring both strength and rigidity. Dorsally the postorbital makes contact with the postfrontal, completing the series, but since their areas of contact are badly damaged nothing can be said of their relationship.

Sloping postero-ventrally from its contact with the postorbital, the quadratojugal terminates in an elliptical cap which is applied to a low protuberance situated ventro-laterally on the quadrate, just above the articular surface. Enclosed by the posterior edge of the quadratojugal and the external edge of the quadrate is a large oval foramen (see fig. 46). In the Lower Triassic thecodont, *Chasmatosaurus*, a similarly placed though much smaller foramen has been interpreted as marking the position of the tympanic membrane (Broili and Schroeder 1934). That this foramen may also have supported a tympanic membrane is rejected, largely on functional grounds (see p. 103).

5. *The adjustment of the palate and its true relationship with the rest of the skull* (figs 37 and 38, plates 7e and 8b)

Having completed the cranial reconstruction, save for the orientation of the otic elements, it should have been possible to adjust the position of the two halves of the palate satisfying all other points of contact between palate and the rest of the skull. Had there been no distortion in the cranial elements this would have been possible, but this was not the case and compromises had to be made, though these did not materially reduce the accuracy of the reconstruction.

The true position of the parasphenoid could not be established directly due to its incomplete nature but sufficient remained to allow a good approximation to be made by extrapolation. A short length of rod was attached to the ventral surface of

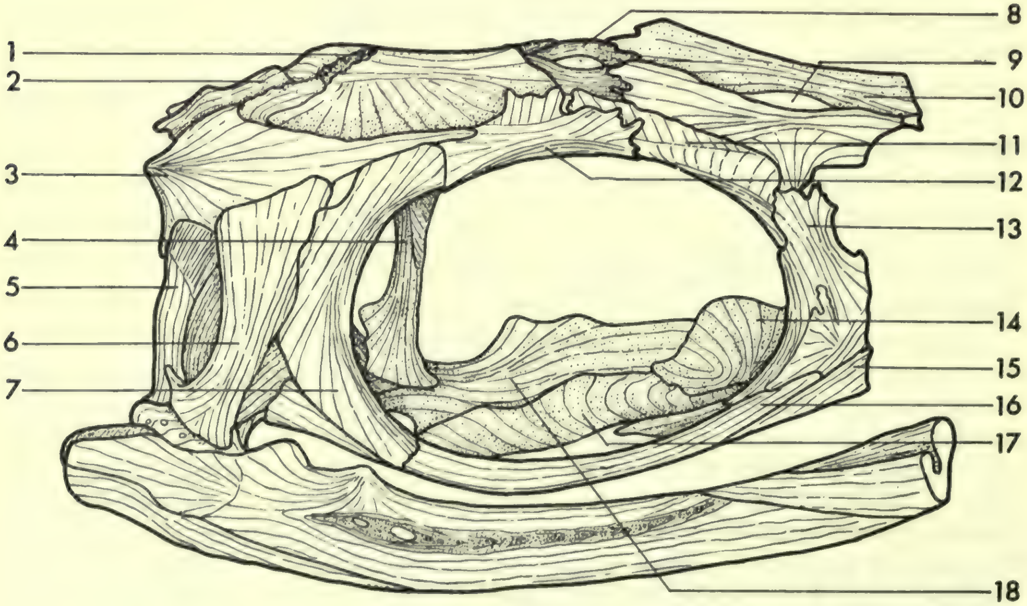

Fig. 37. Skull reconstruction, lateral view, × 1/2 (R8177). 1, parietal ridge. 2, supra-occipital. 3, squamosal. 4, epipterygoid. 5, quadrate. 6, quadratojugal. 7, post-orbital. 8, frontal. 9, internasal foramen. 10, nasal. 11, prefrontal. 12, postfrontal. 13, lachrymal. 14, vomer. 15, maxilla. 16, jugal. 17, palatine. 18, pterygoid.

the parasphenoid, making sure that close contact was maintained along its length, and it was thus demonstrated that the element was situated just above the level of the medial edges of the pterygoids. This conclusion was confirmed by reference to Sollas' serial sections.

6. *The relationship between the otic elements and the rest of the skull*

The relationships between the otic elements and the hind end of the skull was a particularly problematic matter, and one which could only be resolved after the reconstruction of the membranous labyrinth. The main difficulty arises out of the fact that the otic capsule was incompletely ossified, and the three ossifications, (the opisthotic, proötic, and lateral margin of the supraoccipital) were united in cartilage

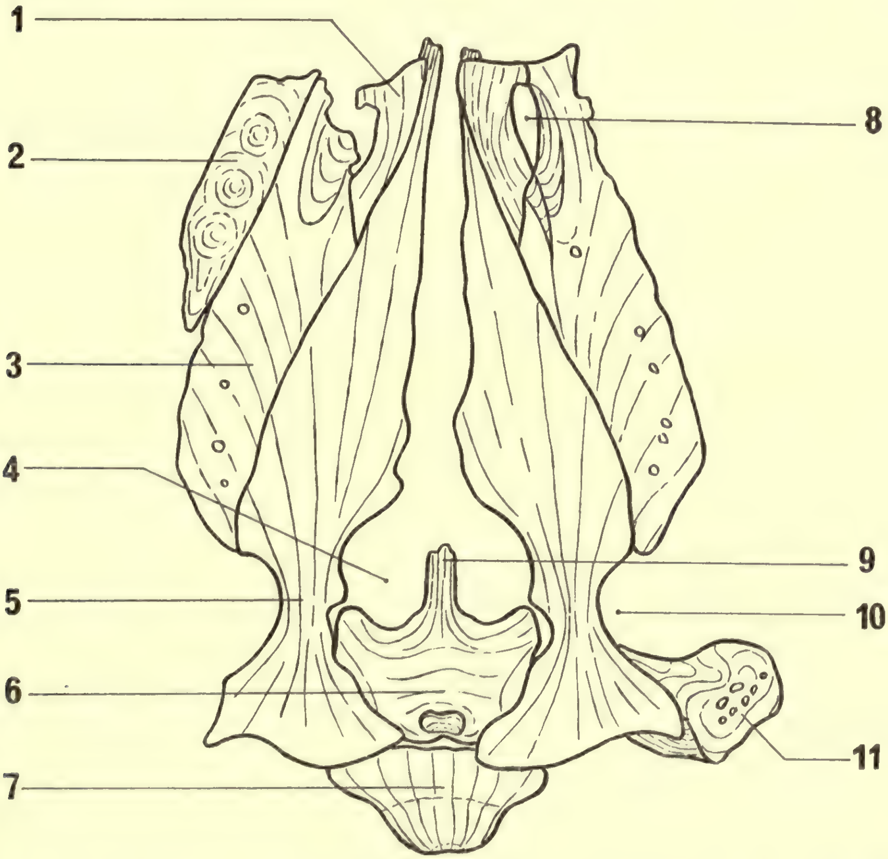

Fig. 38. Reconstruction of the palate, ventral view, articulated with the rest of the skull, ×1/2 (R8177). 1, vomer. 2, maxilla. 3, palatine. 4, interpterygoid vacuity. 5, pterygoid. 6, basisphenoid. 7, basioccipital. 8, internal narial aperture. 9, parasphenoid. 10, intrapterygoid vacuity. 11, articular surface of quadrate.

with no direct contact between them. Fortunately the position of the supraoccipital is well known, so that at least one point on the otic capsule could be fixed. Furthermore the opisthotic has proximal contact with the basioccipital in a fairly well defined articular facet (though a pad of cartilage almost certainly intervened) and distally has a loose contact with the squamosal, providing a second point of reference. The proötic, however, has no contact with any other elements, and its position could only be established by reference to the reconstructed labyrinth.

Even though the stapes has contact with three other elements, the quadrate, opisthotic, and basioccipital, its interpretation has been made difficult by the imprecise nature of its articulations, and also by the intervention of cartilage.

Before postponing further discussion of the otic region until the labyrinth has been considered, it is necessary to consider further the relationships of the opisthotic.

The basioccipital facet of the opisthotic is a shallow triangular depression on the posterior surface, which faces postero-medially. Medial contact with the basioccipital is made, at about the level of the condyle, with the antero-lateral edge. The lateral margin of the basioccipital facet is curved, and slightly raised, and approximates to the curvature of the curved lateral edge of the basioccipital. The two edges do not come into direct contact and it is concluded that the opisthotic was separated from the basioccipital by a thin pad of cartilage. Dorso-ventrally the opisthotic terminates in a rounded paroccipital process which rests loosely in a depression in the squamosal. The surface of this process is quite smooth and has the appearance of an articular condyle (fig. 5).

The account of the cranial reconstruction would be incomplete without description of the snout and upper jaw, and in the absence of sufficient prepared material reference must be made to unprepared skulls and serial sections.

7. *The reconstruction of the snout and upper jaw margin*

The snout, in the context in which the term is used here, commences immediately in front of the orbit, and is formed from the paired nasals, lachrymals, maxillae and premaxillae, the last two mentioned forming the upper jaw margin.

The role of the maxilla in the formation of the upper jaw margin is subordinate to that of the premaxilla, which it meets anteriorly in an oblique suture. The free ventral margins of both elements are grooved for the reception of the teeth, and the groove is both wide and shallow. As the premaxilla encroaches upon the maxilla laterally, it also comes to overlie the nasal. Eventually the dorsal edges of the premaxillae meet in mid-dorsal line, closing over the top of the nasals and hiding them from view. The nasals, however, persist for a considerable distance beneath the premaxillae before finally tapering away.

The dorsal surface of the vomers and pterygoids, which posteriorly form the ventral floor of the snout cavity, are spongy, and each vomer is drawn out dorsally into a thin plate of bone, which, extending vertically into the cavity, bears resemblance to the mammalian turbinal bones.

The external narial aperture lies close to the anterior boundary of the orbit and is surrounded by the lachrymal, nasal, and premaxilla. In some individuals examined the maxilla also participates, but is usually excluded by the union of the maxilla and premaxilla.

Attention will now be turned to the reconstruction of the soft anatomy. As mentioned above it was only after the membranous labyrinth had been reconstructed that the otic elements could be correctly oriented and the skull completed. Consequently the skull reconstruction will be referred to again after the description of the labyrinth.

A RECONSTRUCTION OF THE SOFT ANATOMY

1. *A reconstruction of the membranous labyrinth and its bearing on the orientation of the otic elements*

The correct interpretation of the ichthyosaurian otic region is a problem which has tormented authors past and present, and the key to its solution lies in the reconstruction of the membranous labyrinth.

That it is possible to reconstruct the membranous labyrinth is a reflection of its conservatism throughout the vertebrate series, and the following generalisations may be made.

1. The horizontal semicircular canal lies externally.

2. The ampulla of the horizontal semicircular canal lies in contact with, or close to, that of the anterior vertical semicircular canal.

3. The two vertical semicircular canals have a common origin, or originate close together and high up on the utriculus.

4. The origin of the horizontal semicircular canal lies below that of the two vertical semicircular canals.

5. The anterior and posterior vertical semicircular canals lie at right angles to one another.

6. The horizontal semicircular canal lies predominantly in the horizontal plane (De Beer; 1947).

By reference to these points a generalized labyrinth was modelled and used for comparison during the reconstruction of the ichthyosaurian labyrinth.

Latex casts were taken of the membranous labyrinth impressions of the proötic, opisthotic and supraoccipital and referred to the generalized labyrinth in order that they might be interpreted. The supraoccipital impression is relatively small, rather indeterminate, and also somewhat variable, so that the casts taken were of little value in the reconstruction. The most striking feature about the membranous impressions is that those of the semicircular canals are very wide so that there is barely any differentiation between them and the ampullae. When the otic elements of living reptiles are examined the semicircular canal impressions are found to be very narrow, and the impressions of the ampullae are very many times wider.

The interpretation of the membranous impressions. It is fortunate that the ossifications of the ichthyosaurian otic capsule occurred at points where the canals united with the utriculus, for each ossification conveys a maximum amount of information.

1. *Opisthotic.* In the discussion of the relationships of the otic elements it was pointed out that the relative postion of the opisthotic is quite well known, and it lies with its membranous impression directed anteriorly, and therefore represents the hind-most portion of the otic capsule. The cast obtained is pear-shaped, with a side arm which curves outwards and downwards coming off about half way down its outer margin (fig. 39). There can be little doubt that this arm represents the horizontal semicircular canal, and it would seem that the apical portion represents the origin of the posterior semicircular canal, though it is quite possible that it merely represents the apical portion of the utriculus. Similar conclusions have been drawn elsewhere (Andrews 1910 Appleby 1956 for *Opthalmosaurus*; Sollas 1918 for *Ichthyosaurus*).

2. *Proötic.* The proötic is invariably preserved with its longitudinal axis lying in the horizontal plane and the membranous impression facing inwards, a fact recorded for *Ophthalmosaurus* (Appleby, 1956) and also observed by the present author. Often it lodges between the ascending quadrate wing of the pterygoid and the basisphenoid. These observations have lead everyone to conclude this to be the natural position of the element, and Appleby 1956: 413, comments that while the proötic (of *Ophthalmosaurus*) may have been displaced after death, it is unlikely that it could have turned through an angle as great as a right angle.

The membranous impression of the proötic is ovoid, and has two channels set at right angles. Orientating the element according to Appleby, the horizontal channel is narrower than the vertical, (fig. 40), and is interpreted by Appleby as the horizontal semicircular canal, while the other is concluded to be that of the anterior vertical semicircular canal. Since there are two channels meeting in a right angle,

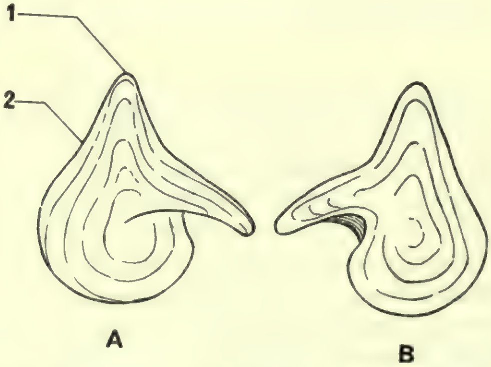

FIG. 39. Latex cast of the membranous impression of the opisthotic (right), × 2 R1168. (A) Posterior view. (B) Anterior view. 1, apex. 2, medial margin.

and since some of the casts show evidence of an ampulla, it seems quite certain that the proötic does indeed mark the point at which the horizontal and the anterior vertical semicircular canals returned to the utriculus, but it was necessary to test the validity of Appleby's orientation.

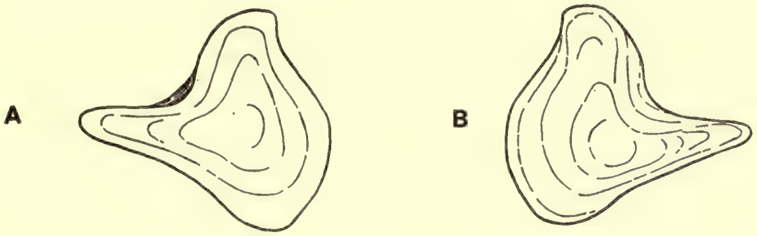

FIG. 40. Latex cast of the membranous impression of the proötic (right), ×2 R1168. Oriented according to Appleby (1956). a, external view. b, internal view.

When a cast of the proötic impression is related with this orientation to the generalized labyrinth, it is found that there is no point of concurrency, and it is not difficult to see the reason why. The horizontal semicircular canal, arising from the utriculus caudally, passes in an external arc to meet the utriculus again anteriorly. Given that the proötic impression represents the anterior point of union of the horizontal semicircular canal with the utriculus, it *must* be orientated with one of its channels pointing caudally to receive it. Rotating the proötic through 90° satisfies this requirement, as shown in fig. 41. Nor is it even necessary to rotate the proötic through as large an angle as 90°, for it is quite probable that the horizontal canal joined the utriculus somewhat obliquely. Furthermore the argument that the proötic could not have rotated through as much as a right angle is really without

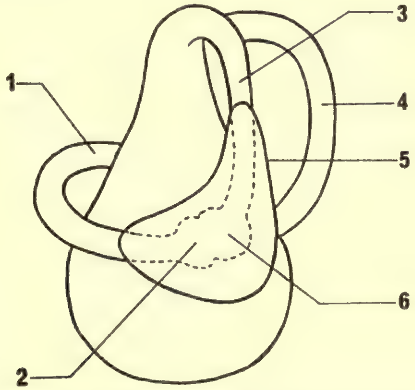

FIG. 41. Anterior view of a generalized membranous labyrinth (right), with the orientation of the proötic set at right angles to that proposed by Appleby. 1, horizontal semicircular canal. 2, ampulla of horizontal semicircular canal. 3, anterior vertical semicircular canal. 4, posterior vertical semicircular canal. 5, proötic. 6, ampulla of anterior vertical semicircular canal.

foundation. The shape of the proötic is such that it can rest on a flat surface in any of several positions, one of which approximates to that in which it is found. If a proötic element is orientated as described here, with the narrowest canal directed vertically, and attached with water-soluble wax to the inside of a beaker which is then filled with water, it will be observed to rotate as it sinks to the bottom. It is therefore concluded that the proötic impression represents the most anterior portion of the membranous lanyrinth. The widest canal is that of the horizontal canal, the narrowest that of the anterior vertical semicircular canal.

The reconstruction of the labyrinth. Since the true shape of the membranous labyrinth can be deduced from only two impressions, the reconstruction of the whole organ is inherently speculative and inferences drawn from its structure correspondingly so. Inasmuch as the reconstructed labyrinth is used here primarily to establish the relationships between the three otic elements, where the relationships of two are already quite well defined, the degree of uncertainty is probably small.

Taking the latex casts of the proötic and opisthotic impressions, the remaining parts of the labyrinth were reconstructed in modelling wax by reference to the generalized pattern. Wax was used because it is one of the few materials to which latex adheres. The thickness of the three canals is known from their impressions in the bone, and some indication of the size of the utriculus is given by the opisthotic impression. Having produced a labyrinth comforming to these requirements, (fig. 42) the opisthotic and proötic were attached, and the whole structure was tentatively

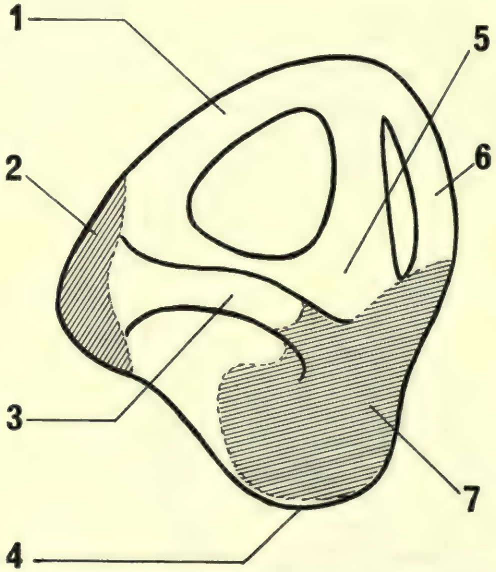

FIG. 42. Reconstruction of the membranous labyrinth, (left), external lateral view, × 2 (based largely on Evans' nodule). Shaded areas represent latex impressions. 1, anterior vertical semicircular canal. 2, proötic impression. 3, horizontal semicircular canal. 4, saccular portion of labyrinth. 5, utricular portion of labyrinth. 6, posterior vertical semicircular canal. 7, opisthotic impression.

positioned at the back of the skull. The amount of space available for accommodation of the otic capsule is limited, and the nascent labyrinth had to be reduced in size in order that the capsule might fit. From the position of the supraoccipital relative to the rest of the otic capsule it was apparent that it must have roofed the labyrinth.

The otic impression in the supraoccipital is somewhat triangular, with its long side lying almost horizontally, and from its position it seems reasonable to conclude that it represents the point at which the two vertical canals took origin from the apex of the utriculus (fig. 43). In the largest ex-nodular specimen, R8177, the impression is relatively small and deep, and probably embraced the apical tip of the utriculus, the two vertical canals taking origin below this level. However, in R3375, a specimen of comparable size, the impression is like that of the smaller skulls. After a number of trials and modifications a satisfactory reconstruction was obtained (fig. 44).

The impression of the labyrinth in the opisthotic shows no indication of a constriction between a saccular and utricular portion, and the sacculus is apparently represented by the rounded ventral portion of the labyrinth. Ventrally this saccular portion lies above the stellate excavation of the basioccipital and it seems probable that this marks the position of a small lagena. A small depression lying just beneath the level of the main depression of the opisthotic probably also contributed.

2. *A reconstruction of the cartilaginous walls of the otic capsule*

The bone circumscribing the otic impressions of the three otic elements has the familiar indentation pattern indicative of a cartilage junction where it was continuous with the cartilaginous wall of the otic capsule, and the thickness of this wall can readily be determined. The wall was thickest in the supraoccipital region, and, reducing anteriorly and ventrally, was thinnest in the proötic. By joining the bony edges with thin sheets of Plasticine the cartilaginous walls were reconstructed, and the three otic elements were united with the exoccipital in a most satisfactory relationship (fig. 45). The longitudinal ridge of the leading edge of the exoccipital was clearly demonstrated to be continuous with the cartilaginous otic wall. Furthermore, the smooth dorsal surface which lies outside articular contact with the supraoccipital bears some evidence of a depression which corresponds to the course of the posterior vertical semicircular canal (fig. 44a). The internal curvature of the supraoccipital arch is continued by the internal wall of the otic capsule and forms the lateral wall of the chondrocranium. A cartilaginous pad of moderate thickness must have intervened between the opisthotic and basioccipital, and this was probably continuous with the catilaginous posterior margin of the otic capsule, and perhaps also with the pad between the exoccipital and basioccipital. The successful reconstruction of the otic capsule is reciprocal confirmation of the validity of the labyrinth, and now that the otic elements had been oriented, the stapes could be put into position completing the cranial reconstruction.

The orientation of the stapes. The stapes is a fairly stout element which forms a strut between the otic capsule proximally and the quadrate distally. The opisthotic

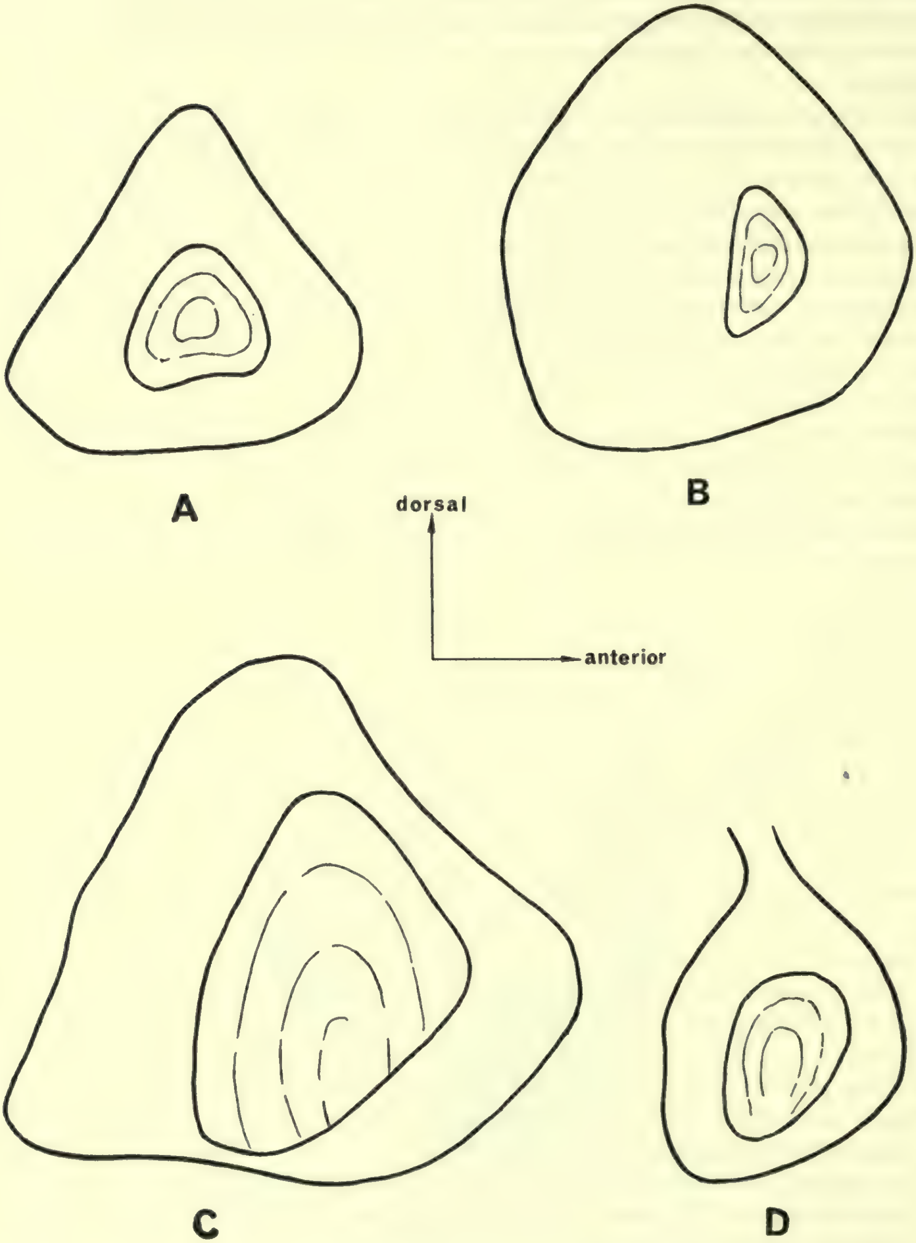
A
B
dorsal
anterior
C
D

Fig. 43. Membranous impression of the supraoccipital in different specimens (external view, right side), all to same scale ×3. a, Evans' nodule. b, R8177. c, R3375. d, R6697.

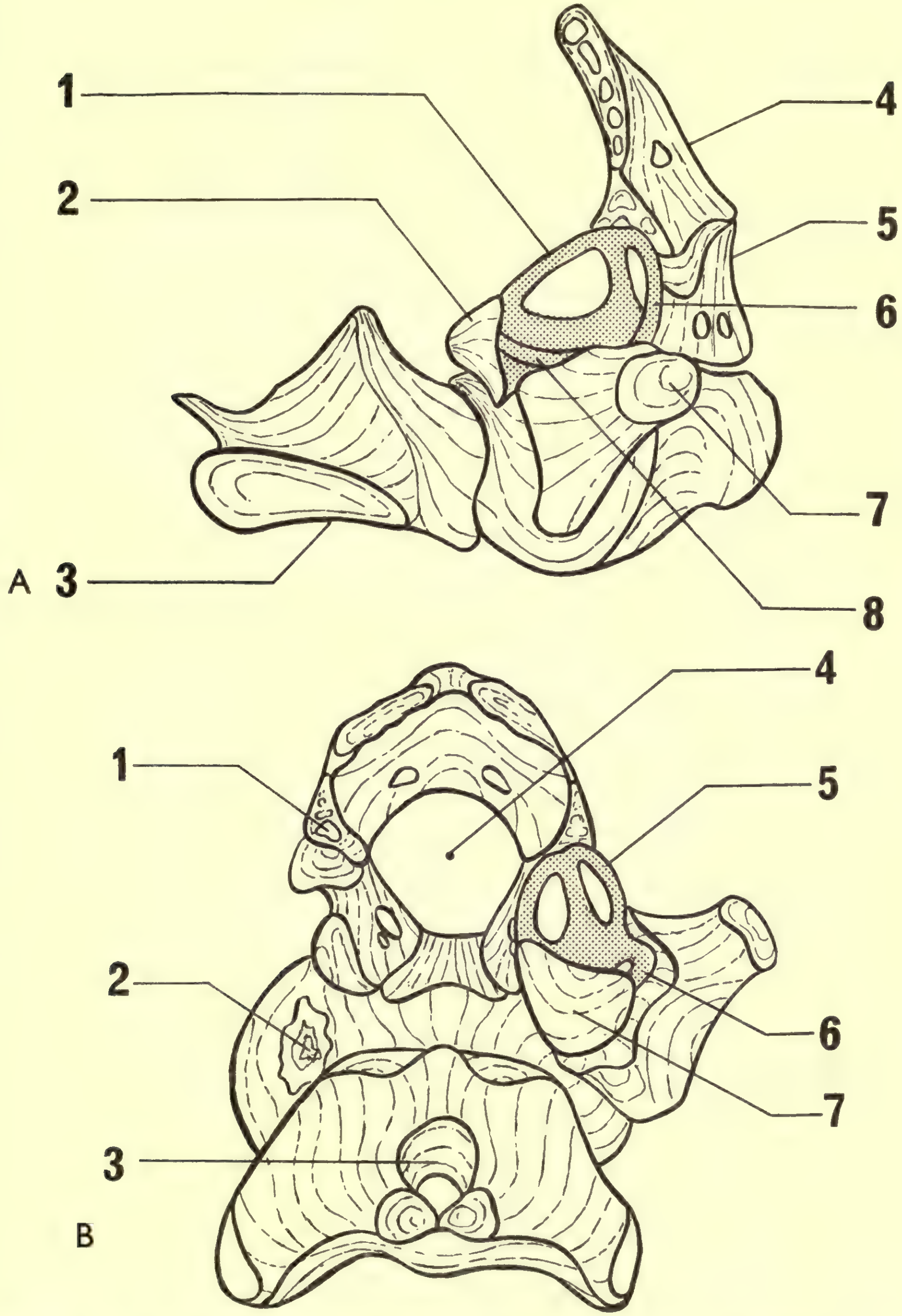

FIG. 44. (a). Reconstructed occiput with a reconstruction of the membranous labyrinth (left side), external lateral view × 1 (Evans' nodule). 1, anterior vertical semicircular canal. 2, proötic. 3, basisphenoid. 4, supraoccipital. 5, exoccipital. 6, posterior vertical semicircular canal. 7, paroccipital process of opisthotic. 8, horizontal semicircular canal. (b). Reconstructed occiput with a reconstruction of the membranous labyrinth (left side), anterior view × 1 (Evans' nodule). 1, membranous impression of supraoccipital. 2, stellate excavation of basioccipital. 3, carotid foramen. 4, foramen magnum. 5, posterior vertical semicircular canal. 6, horizontal semicircular canal. 7, proötic.

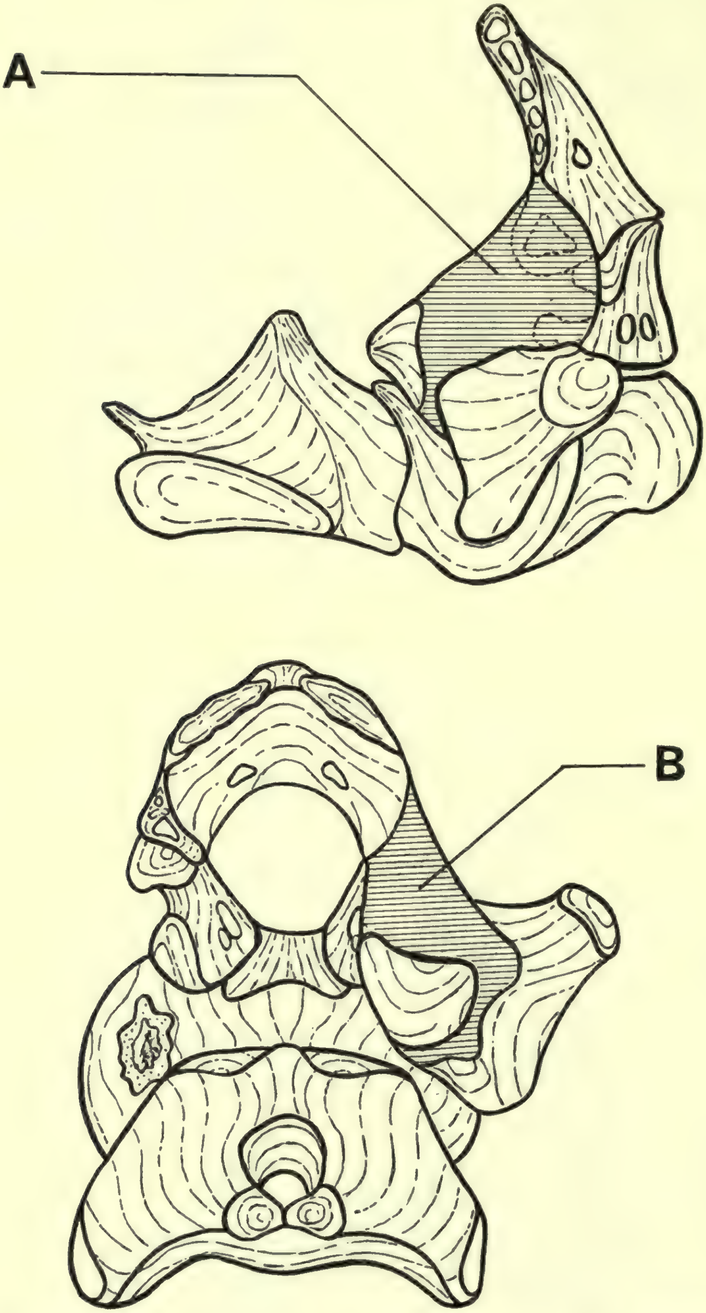

FIG. 45. (a). Reconstructed occiput with a reconstruction of the cartilaginous otic capsule (left side), external lateral view × 1 (Evans' nodule). (A) Cartilaginous otic capsule. (b). Reconstructed occiput with a reconstruction of the cartilaginous otic capsule anterior view, × 1 (Evans' nodule). (B) Cartilaginous otic capsule.

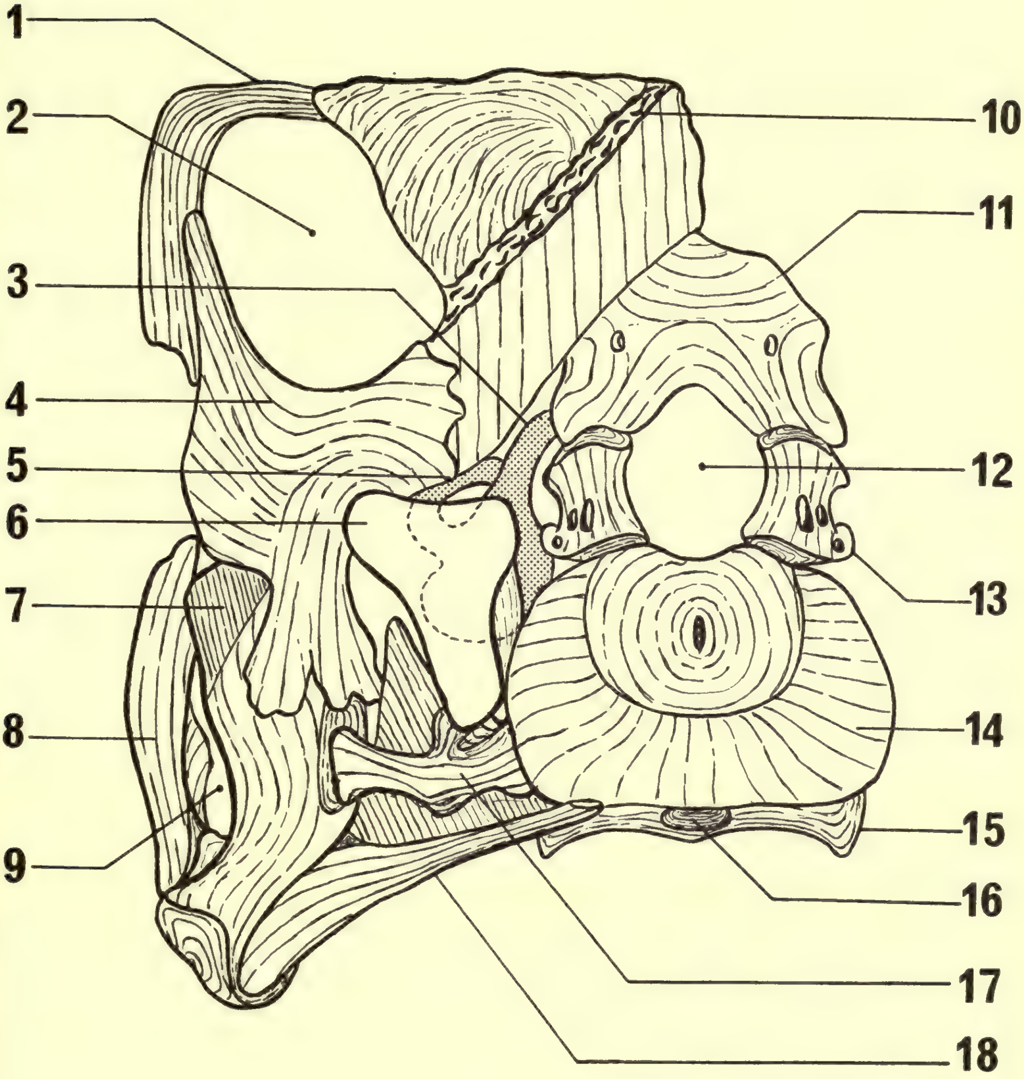

FIG. 46. Skull reconstruction, posterior view, with reconstructed membranous labyrinth, ×4/3, based largely on R6697. 1, postfrontal. 2, temporal vacuity. 3, posterior vertical semicircular canal. 4, squamosal. 5, horizontal semicircular canal. 6, opisthotic. 7, quadrate. 8, quadratojugal. 9, oval foramen. 10, parietal ridge. 11, supraoccipital. 12, foramen magnum. 13, exoccipital. 14, basioccipital. 15, basisphenoid. 16, carotid foramen. 17, stapes. 18, medial wing of pterygoid.

facet on the postero-dorsal aspect of the head is but a shallow depression and it is therefore not possible to obtain a positive relationship between these two elements. There is a similar degree of freedom existing between the stapes and quadrate, and a pad of cartilage almost certainly intervened. No information is forthcoming from the relationship between the basioccipital and stapes because they make only touch contact, no evidence of articular surfaces being apparent. However, in most of the material examined there is a well marked groove for the stapedial artery and this has been a particularly important factor in arriving at a solution to the problem.

The stapedial artery is a branch of the carotid and passes through a notch or groove in the head of the stapes before gaining access to the endocranial cavity. The stapes therefore had to be oriented with the groove directed obliquely forward and inward. On the anterior face of the head, just below the level of the stapedial artery groove, there is, in smaller specimens, a concave facet which has been interpreted as that part of the footplate which inserted into the fenestra ovalis. This facet therefore has to be directed towards the saccular region of the reconstructed labyrinth thus offering another point of reference. There is no direct evidence of a fenestra ovalis since the otic capsule is not ossified in this region. Five reference points are therefore available for the orientation of the stapes, and although in each there is an amount of freedom, considered together they establish the position of the stapes with a good degree of confidence thus completing the skull (Fig. 46, plate 7d.)

Distally the stapedial shaft widens and terminates in an oval facet whose oblique face lies parallel with a depressed area on the postero-medial surface of the quadrate. As previously mentioned, direct contact with the quadrate does not seem to have been made and it seems quite certain that the stapedial shaft was continued in cartilage. The stapedial facet on the quadrate is wider than the distal facet of the stapes and the cartilaginous extension of the stapes was probably expanded to fill it.

Having completed the account of the membranous labyrinth and its implications, attention can be turned to a reconstruction of the brain and cranial nerves.

3. *A reconstruction of the brain and cranial nerves*

The brain

The fact that the reptilian brain (fig. 47) lies loosely within the cranium, not filling it to nearly the same extent as in the mammal, is well established and requires no further amplification here. It was therefore with caution, tempered with a degree of scepticism, that the possibility of reconstructing the brain was examined. Since the ichthyosaurian skull contained so much cartilage that the sides and much of the cranial floor cannot be reconstructed, it would not have been altogether unreasonable to dismiss the matter, but the fact remains that the skull roof bears four distinct encephalic impressions and these had to be interpreted (fig. 48).

There are a number of points of reference on the skull which permit the positions of the lobes of the brain to be established, hence the encephalic impressions of the skull roof could be interpreted. These points are listed below.

1. The posterior limit of the brain is marked dorsally by the supraoccipital arch,

laterally by the exoccipital foramen for the hypglossal nerve, and ventrally by the diverging portion of the median basioccipital excavation.

2. The position of the ventral flexure of the hindbrain is marked by the descending basioccipital peg and the ascending dorsal surface of the basisphenoid (fig. 44a, plate 7b).

3. The position of the junction between the fore- and midbrain is approximated dorsally by the pineal foramen, and ventrally by the sella turcica.

4. The proötic, being the most anterior part of the otic capsule, indicates the approximate level of the facial nerve (the otic capsule lies between facial and glossopharyngeal in all craniates), and hence the anterior limit of the hindbrain (fig. 44a).

5. The trigeminal nerve arises at a level which is posterior to that of the epipterygoid (the epipterygoid separates the profundus from the maxillary branch of the trigeminal), and, since the trigeminal takes origin from the anterior portion of the hind brain, it follows that the hindbrain must lie wholly behind the level of the epipterygoids.

6. The level of the external narial aperture approximately indicates the anterior limit of the brain.

The four encephalic impressions in the skull roof were clearly demonstrated by making a latex cast (fig. 49). The most prominent of these is formed by the parietals at the level of the epipterygoid process. This is not a single impression but is paired, and the two halves are formed by the two parietals, separated by a low ridge in the midline. The two impressions are ovoid, their longitudinal axes lying approximately parallel with that of the skull, and are deepest in front, becoming shallow caudally. The external lateral margin is formed in part by the medial surface of the epipterygoid process, and is continued posteriorly by a ridge which

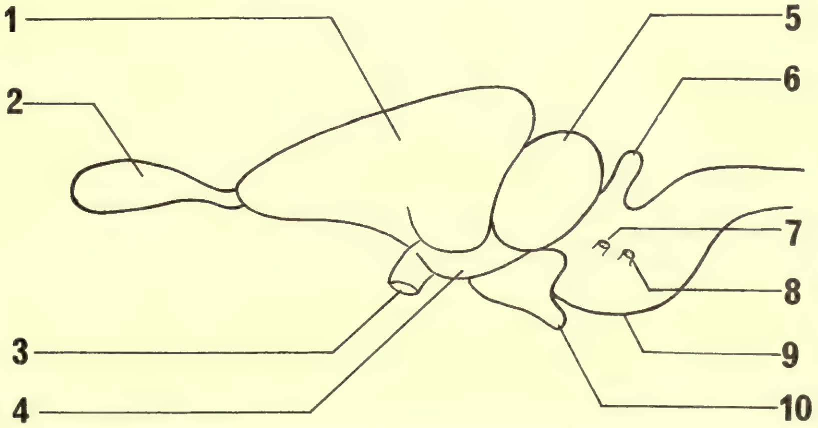

FIG. 47. Brain of *Lacerta* (left side), external lateral view. 1, cerebral hemisphere. 2, olfactory lobe. 3, optic nerve. 4, optic tracts. 5, optic lobe. 6, cerebellum. 7, 5th cranial nerve. 8, 7th cranial nerve. 9, medulla oblongata. 10, pituitary. (After Parker).

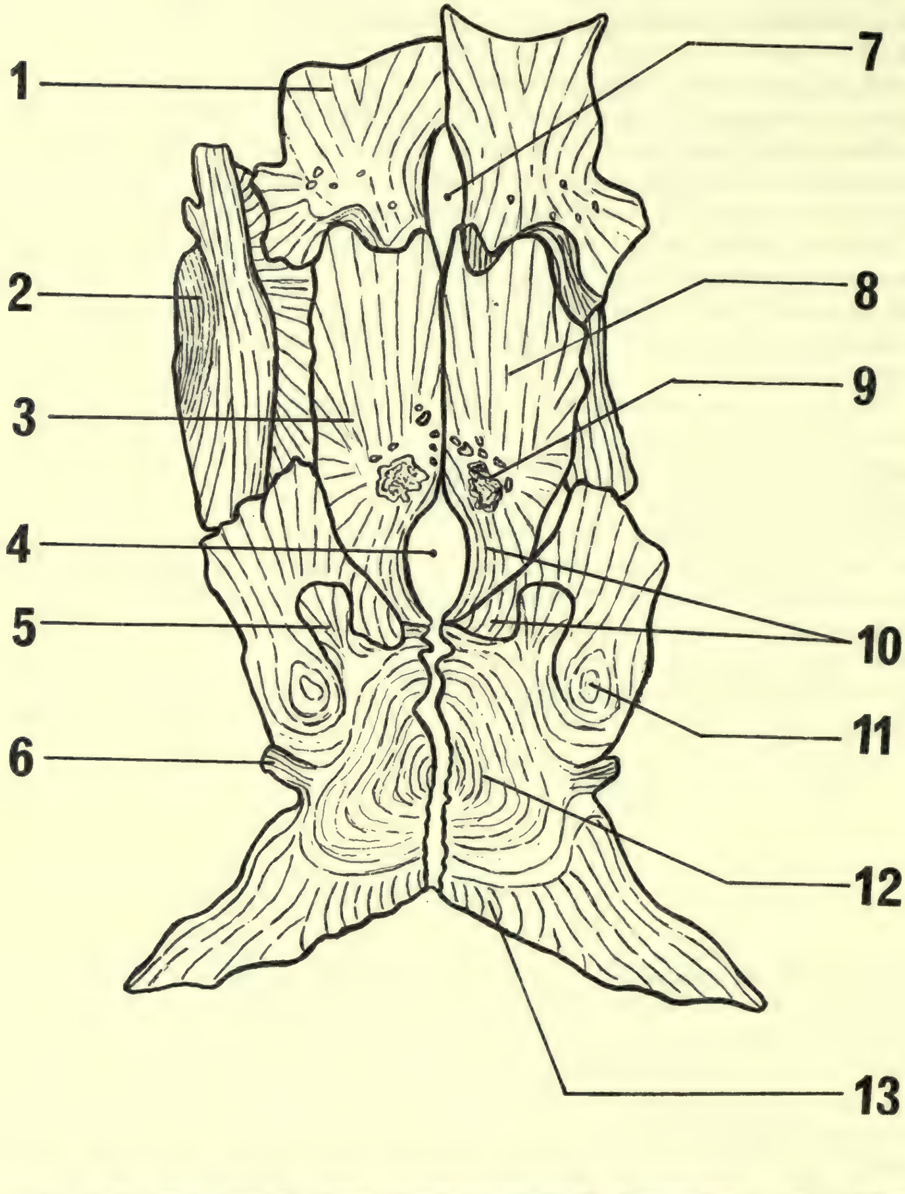

FIG. 48. Skull roof, ventral view, showing encephalic impressions, ×3/4 (R8177). 1, nasal. 2, prefontal. 3, frontal. 4, pineal foramen. 5, descending parietal flange. 6, epipterygoid process. 7, internasal foramen. 8, impression of olfactory lobe. 9, foraminous area. 10, impression of cerebral hemisphere in frontal and parietal. 11. extraencephalic depression. 12. impression of optic lobe. 13, impression of cerebellum.

then curves towards the midline to form the posterior margin. In front of the epipterygoid process the lateral margin is formed by a bony lip, which is also the external margin of a lateral extra-encephalic depression, and which is continuous with the external edge of the descending parietal flange. The anterior margin is marked by an almost straight and transverse ledge which is the ventral edge of a prominent bony buttress formed by the thickened leading edge of the parietals. The posterior margin lies close to the posterior edge of the parietals, but is separated by a narrow ledge of bone which bears evidence of a second and unpaired depression.

The second encephalic impression is very shallow and indistinct, but its presence was confirmed by the latex cast. When compared with a cast taken of the internal

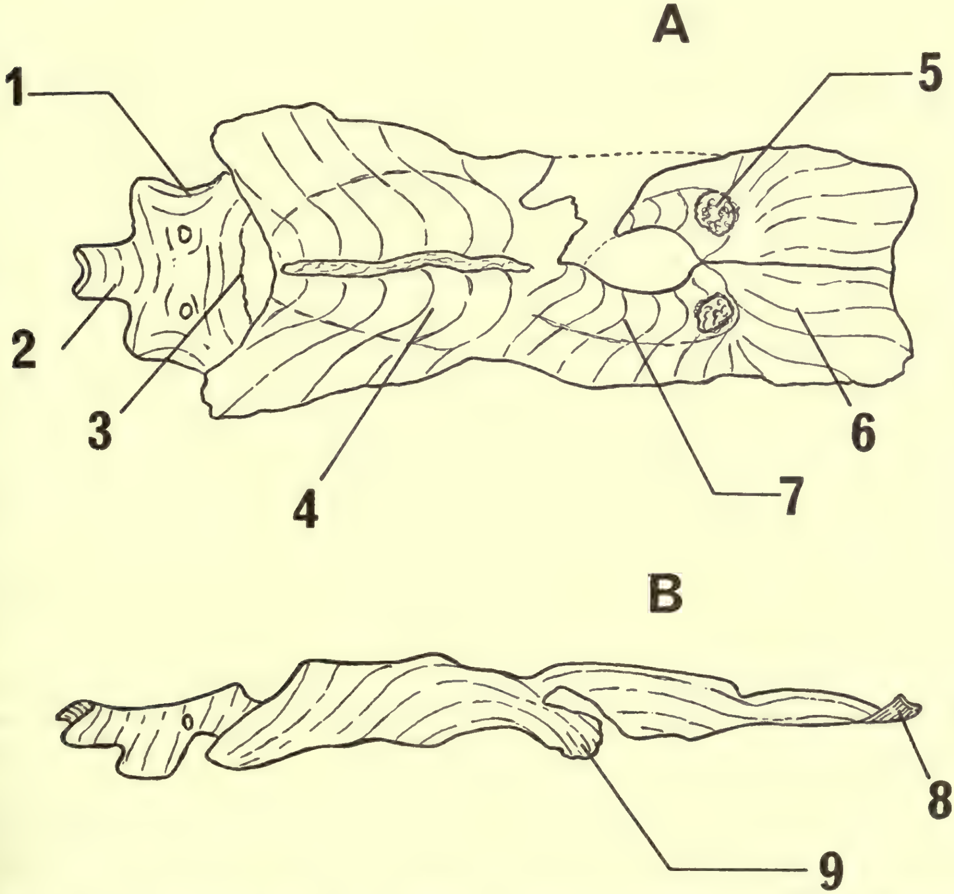

Fig. 49. Latex encephalic cast, ×3/4 R8177. (A) Dorsal view. (B) Lateral view (right side). 1, cast of supraoccipital impression. 2, spinal cord. 3, cerebellum. 4, optic lobe. 5, foraminous area. 6, olfactory lobe. 7, cerebral hemisphere. 8, upturned thin leading edge of cast. 9, cast of descending parietal flange.

surface of the supraoccipital, similarities were found both in the overall width, and in the radius of curvature, and it was concluded that the two impressions embraced the same encephalic structure. Because of its posterior position, its continuity with the spinal cord, and its unpaired nature, there can be no doubt that this impression embraced the dorsal surface of the hindbrain, and from its position it must represent the cerebellum. By reptilian standards this was very large. However, it would be expected that the ichthyosaur, so highly adapted to the aquatic environment, would have a well developed cerebellum, and in this respect they compare with the cetaceans where the cerebellum is better developed than in other mammals (Slijper 1962). The ventral portion of the hindbrain rests in the depression formed by the descending basioccipital peg and the ascending dorsal surface of the basisphenoid (fig. 44). Caudally this depression is continuous with the median longitudinal channel of the dorsal basioccipital surface, which supported the spinal cord.

Having unequivocably established the position of the hindbrain it was concluded that the paired parietal depressions, which lie immediately anterior to that of the cerebellum, embraced the optic lobes of the midbrain. That these depressions might have embraced the cerebral hemisphere can be immediately dismissed because they lie too far back, and because there is anyway a second pair of depressions directly anterior to them (these lie largely in the frontals), which are interpreted as the cerebral hemisphere impressions. The optic lobes are the most prominent of the cerebral structures, a reflection of the large size of the eyes, and confirmation of the conclusion already reached that vision was the predominant sense. The descending parietal flanges no doubt gave mechanical support to the large optic lobes. The paired impressions of the cerebral hemispheres are jointly formed by the parietals and frontals, and between these two impressions is the pineal foramen.

The impression of the cerebral hemisphere is oval and of comparable length to that of the optic lobe, though narrower and more strongly arched. At the apex of each there is a rounded foraminous area of unknown significance. A similar area is found posteriorly, and is underlain ventrally by the proximal portion of the descending parietal flange. The pineal organ in ichthyosaurs is atypical in its posterior position, being flanked on either side by the cerebral hemispheres, and, judging by the large size of the foramen, it was probably photosensitive. The last of the cerebral impressions are a pair of shallow depressions which lie in the anterior half of the frontals and which are interpreted as roofing the olfactory lobes.

From the shallow nature of their impressions in the bone, it would seem a reasonable inference that the olfactory lobes were not extensive. Somewhat rectangular in outline, the impressions become shallower rostrally, finally flattening at a level just posterior to the external narial aperture (fig. 49b).

By reptilian standards the brain was extensive, and in specimen R8177 the brain had a length of about 13 cm which is about one-third of the skull length. The cerebral architecture was overshadowed by the prominence of the optic lobes, which probably accounted for almost half of the total volume. The cerebellum was very large, a condition which is indicative of a high level of locomotor integration. The cerebral hemispheres were relatively large and swollen, somewhat similar to the avian condition where the enlarged corpora striata are responsible for their rotundity.

The corpus striatum is the seat of innate behavioural activity and it seems reasonable to conclude that the ichthyosaur possessed a wide spectrum of instinctive behavioural patterns.

From observations of specimens in which the remains of unborn offspring are preserved it is clear that few were born at any one time and these were delivered from the cloaca tail first. The birth would certainly have been attended by a considerable degree of parental care, and may also have been accompanied by displays of social co-operation by other individuals. It is very probable that ichthyosaurs were gregarious and some evidence for this is available from Germany where aggregations of specimens have been found in some quarries. The gregarious habit is associated with co-operative behaviour which is further evidence of cerebral activity at a high centre.

The olfactory lobes were relatively small and the significance of this is discussed below (see section titled–*Olfaction*).

The cranial nerves. Little is known of the cranial nerves since only four nerve foramina are preserved in bone, all of which pierce the exoccipital (fig. 3, plate 1c).

Since the exoccipital is the most posterior portion of the cranial wall its posterior foramen is concluded to be that for the exit of the hypoglossal nerve. Immediately anterior to this is a second foramen of comparable size which was for the exit of a second branch of the hypoglossal, or for the exit of the spinal accessory, or a branch of the vagus nerve. Since the spinal accessory is usually a relatively small nerve and usually passes out with the vagus by way of the jugular foramen (Romer 1956), the first possibility is the least likely. Furthermore, since the bone passages of the two posterior foramina tend to converge medially it seems reasonable that they conducted a pair of nerves whose origins were in close proximity, and it is therefore concluded that the second foramen conducted another branch of the hypoglossal.

The largest of the foramina, the jugular foramen, is not completely circumscribed in bone. In addition to transmitting the internal jugular vein, the jugular foramen served for the passage of the vagus nerve, probably the glossopharyngeal, and perhaps also the spinal accessory. Just beneath the jugular foramen is the last and smallest of the nerve foramina which might well have conducted the spinal accessory nerve.

4. *A reconstruction of the mandibular musculature*

The mandibular muscles have been classified by Luther (1914) according to their function and position relative to the trigeminal nerve. Three groups of mandibular muscles have been recognized; the adductor mandibulae group which serve to close the jaws, the constrictor dorsalis group which is developed in kinetic skulls for the purpose of elevating and moving the maxillary segment relative to the occipital segment, and the constrictor ventralis group which, passing between the mandibular rami, aids swallowing and respiratory movements (see also Edgeworth, 1935). The reptilian abductor muscle, the *M. depressor mandibularis*, which opens the jaws is innervated by cranial nerve 7 and belongs to the hyoidean branchial muscle division, but for convenience it will be discussed here.

The reconstruction of the mandibular musculature in fossil forms is beset with problems because of the difficulties in recognizing muscle attachment areas and because of the variations from one species to another. The problem is further aggravated in the Ichthyosauria by the complete absence of knowledge of the trigeminal nerve. Since the adductor muscles are identified according to their positions relative to this nerve, the present reconstruction cannot claim to be anything more than a tentative solution of the problem.

The mandibular rami do not bear any obvious muscle scars of the constrictor ventralis group, nor is there evidence of muscles of the constrictor dorsalis division, so that the present account is restricted to the adductor mandibulae group.

The adductor mandibulae group. The adductor mandibulae group is divisible into three parts according to position relative to the trigeminal nerve.

1. The *M. adductor mandibulae externus* division which lies between the maxillary and mandibular branches of the trigeminal, and which is in turn subdivided into three:

    a. *M. adductor mandibulae externus superficialis*
    b. *M. adductor mandibulae externus medialis*
    c. *M. adductor mandibulae externus profundus*

2. The *M. adductor mandibulae internus* division lies medial to the maxillary branch of the trigeminal nerve, and has two components:

    a. *M. adductor mandibulae internus pseudotemporalis*
    b. *M. adductor mandibulae internus pterygoideus*

3. The *M. adductor mandibulae posterior* division which lies medial and posterior to the mandibular branch of the trigeminal nerve, and which is usually not subdivided.

While the mandibular insertions of the adductor muscles are usually prominent and well delimited, their cranial origins are less well defined and individual identities cannot be established.

The mandibular muscle insertion areas (fig. 25). Four insertion areas for the mandibular muscles can be discerned in the lower jaw. Anteriorly there is the coronoid process, a low swelling of the dorsal margin of the surangular which is finely marked by small pits and which has a triangular outline when viewed from above. Posteriorly and still on the surangular is the 2nd insertion, a triangular, dorso-medially inclined area, which is coarsely marked by denticulate processes, and which is produced rostrally into an antero-medially inclined and sharp crest. The third insertion is a depressed area on the external surangular surface which lies, for the most part, just posterior to the last mentioned insertion, and is largely retroarticular in position. Superficially it is sculptured by fine longitudinal striae which have a tendency to converge antero-ventrally. The fourth is the least well defined area and lies on the retroarticular surface of the angular and perhaps also on the terminal portion of the surangular where its boundaries with the previous mentioned insertion become indefinable. It is marked superficially by fine striations which become indistinct anteriorly. The floor of the Meckelian canal bears little evidence of any muscle scars, but this is frequently the case for this particular insertion area and it was almost certainly a place of muscle attachment.

The identities of the muscle insertions outlined above were investigated by a comparison with extant reptiles, and the origins and insertions of the mandibular muscles in various reptiles is contained in Table 2.

Table 2

CRANIAL MUSCULATURE

A. *MANDIBULAR MUSCULATURE*

Three groups of mandibular muscles can be recognized:

Adductor Mandibulae Group	*Constrictor Dorsalis Group*	*Constrictor Ventralis Group*

Adductor Mandibulae Group

This group is divisible into three parts:

M. adductor mandibulae externus	*M. adductor mandibulae internus*	*M. adductor mandibulae posterior*

M. adductor mandibulae externus

This muscle is divisible into three parts:

M. adductor mandibulae externus superficialis	*M. adductor mandibulae externus medialis*	*M. adductor mandibulae externus profundus*
Typically originates from the inner surface of the ventral boundary of the upper temporal vacuity in diapsids, and passes ventrally, inserting on the lower jaw posterior to the level of the coronoid process.	Originates from and inserts into a similar place to that of the *superficialis*. In *Spenodon* the origin is reduced and the major area of attachment is on the dorso-lateral surface of the braincase.	Originates from the lateral wall of the cranium on the squamosal. This is the deepest portion of the *externus* and fills much of the upper temporal vacuity and usually has a common area of insertion with the other parts.

M. adductor mandibulae internus

This muscle is divisible into two parts:

M. adductor mandibulae internus pseudotemporalis	*M. adductor mandibulae internus pterygoideus*
This is frequently the largest of the temporal muscles in living reptiles and originates from the lateral surface of the cranium in the anterior portion of the upper temporal vacuity. Its area of insertion usually lies on the coronoid process.	This muscle may have a double origin being divisible into a *pterygoideus dorsalis* and a *pterygoideus ventralis*. The *pterygoideus ventralis* takes origin from the posterior surface of the pterygoid ventral to the basipterygoid process, while the *pterygoideus dorsalis* originates from the maxilla. The insertion of the *pterygoideus* is quite constant in living reptiles and lies on the lateral and medial surfaces of the retroarticular process so that part of the muscle wraps around beneath the jaw ramus.

TABLE 2 (*contd.*)

M. adductor mandibulae posterior

This is a single muscle which typically originates from the anterior surface of the quadrate and inserts in the intramandibular fenestra.

Constrictor Dorsalis Group

This group is largely concerned with raising and moving the palatal region relative to the rest of the skull and is found in kinetic forms. Three divisions have been described, *M. protractor pterygoidei*, the *M. levator pterygoidei*, and the *M. levator bulbi*. The first two muscles are concerned with kinetic movements and are developed only in kinetic forms.

M. levator pterygoidei

In *Sphenodon* this muscle takes origin from the ventrolateral wall of the orbitosphenoid, medial to the dorsal extremity of the epipterygoid. This is a narrow muscle which lies medial to, and runs parallel with, the epipterygoid shaft, inserting on the dorsal and medial part of the pterygoid and on the lower part of the medial surface of the epipterygoid.

M. protractor pterygoidei

In *Sphenodon* this muscle originates from the ventrolateral surface of the proötic and passes posteroventrally as a broad sheet which inserts on the dorsal margin of the quadrate process of the pterygoid. Ostrom (1962), has shown that the development of the *levator* and *protractor* muscles in *Sphenodon* varies from individual to individual.

M. levator bulbi

This is a very problematic muscle which is well developed in most living reptiles and which takes origin from the lateral cranial wall.

Constrictor Ventralis Group

This group is represented by the *M. mylohyoideus* which generally has the form of a superficial sheet of muscle between the lower jaw rami. The *M. mylohyoideus* is present in all living forms and is developed to a variable extent. In the crocodile it is a single sheet of muscle which extends from the posterior portion of the jaw to the symphysis, while in *Sphenodon* and certain lizards it is divided into two sheets, one anterior to the other.

B. *BRANCHIAL MUSCULATURE*

Included in this group is the abductor muscle which closes the jaws, *M. depressor mandibulae*. This is a conservative muscle which usually has its origin in the dorsal occipital region and inserts upon the rectoarticular process of the lower jaw.

From this it is concluded that the coronoid process is the insertion area of the *M. adductor internus pseudotemporalis*, and that the dorso-medially inclined insertion area was for the three parts of the *M. adductor mandibulae externus*.

The extensive retroarticular area on the external surface of the surangular was for the insertion of the depressor muscle, while the *M. adductor mandibulae internus pterygoideus* inserted on the retroarticular portion of the angular.

The slightly sunken insertion area of the depressor muscle is continued forward by a tapering furrow which extends to the posterior level of the coronoid process, and its ventral boundary is raised forming an oblique bony ledge (fig. 25a7). It is possible that part of the *M. adductor mandibulae externus* inserted into this ledge, though nothing more definite than this can be said at the present time. Having as far as possible interpreted the mandibular insertions it was necessary to establish the origins of the muscles.

The mandibular muscle origins (fig. 50)

1. *M. adductor mandibulae externus* (fig. 51a, b and c)

The outer rim of the temporal vacuity is formed by the lateral limb of the squamosal. On its inside surface is a low ridge which, commencing at the anterior tip, slopes slightly ventrally as it passes back almost to the posterior margin of the vacuity. Because of the convexity of the squamosal wall the dorsal lip of the vacuity lies medial to this ridge. It is thought that this ridge was the origin of the *superficialis* division, whilst the *medialis* division took origin from the dorsal lip of the vacuity. These two almost vertical sheets of muscle probably filled the lateral sector of the temporal vacuity, converging ventrally to insert on the surangular.

The *profundus* division is the deepest part of the *M. adductor mandibulae externus*, and typically lies medially, filling the posterior portion of the vacuity. The rugosity of the parietal ridge, which is continued on the squamosal, is taken to mark the origin of this muscle, (fig. 52c).

2. *M. adductor mandibulae internus* (fig. 51d and e)

The *pseudotemporalis* division is frequently the largest of the temporal muscles and fills the anterior portion of the vacuity. The dorsal surface of the parietal bears a shallow depression, which, commencing just in front of the parietal ridge, is continued forward up to the anterior edge. This is interpreted as the origin of the *pseudotemporalis* muscle. The antero-lateral corner of the parietal is roughened but it cannot be established whether this is due to poor preservation or whether this too formed part of the origin. The *M. adductor mandibulae internus pterygoideus* took its origin somewhere on the pterygoid, probably anterior to the basipterygoid region, but in the absence of very obvious muscle scars any further discussion would be speculative. In living reptiles the pterygoideus wraps around beneath the mandible to insert upon the external surface of the retroarticular process, and there seems no reason to doubt a similar course for this muscle in ichthyosaurs (fig. 51e).

3. *M. adductor mandibulae posterior* (fig. 51f)

In the typical reptilian condition this muscle originates from the anterior surface of the quadrate and inserts in the Meckelian canal, and this position is assumed for the ichthyosaurs. The anterior surface of the quadrate is hollowed and in some speci-

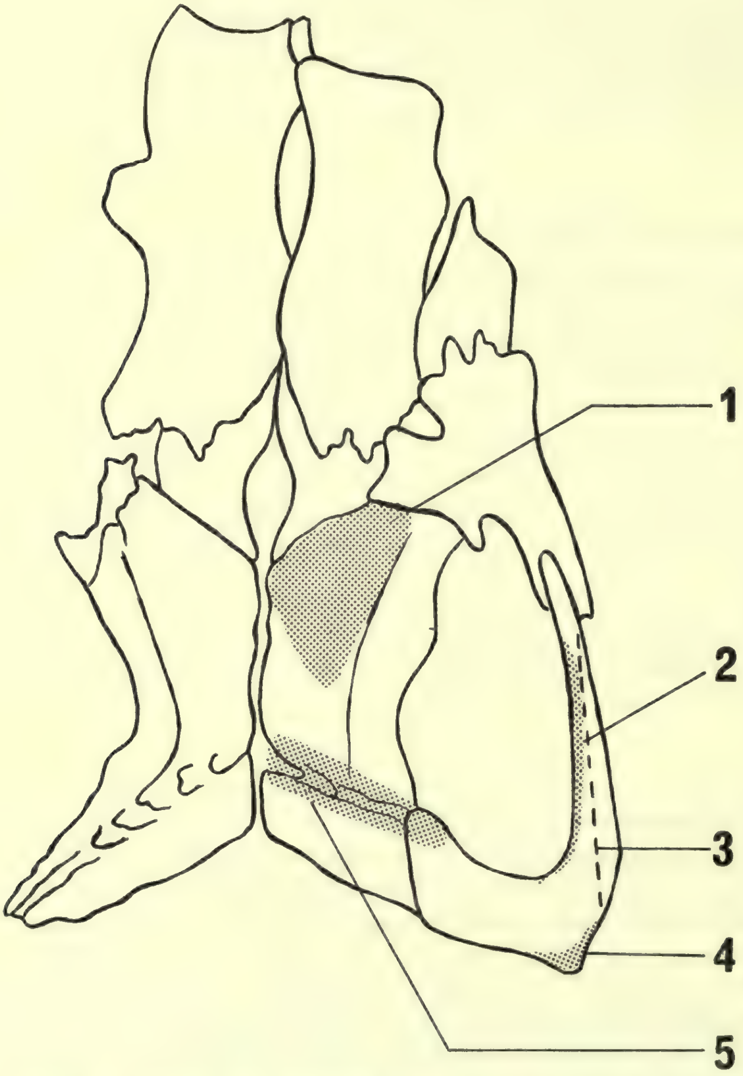

FIG. 50. Skull roof, dorsal view, showing approximate positions of the origins of the mandibular muscles, × 2/3 (R8177). 1, origin of the *M. adductor mandibulae internus pseudotemporalis*. 2, origin of the *M. adductor mandibulae externus medialis*. 3, position of the origin of the *M. adductor mandibulae externus superficialis*. 4, origin of the *M. depressor mandibulae*. 5, origin of the *M. adductor mandibulae externus profundus*.

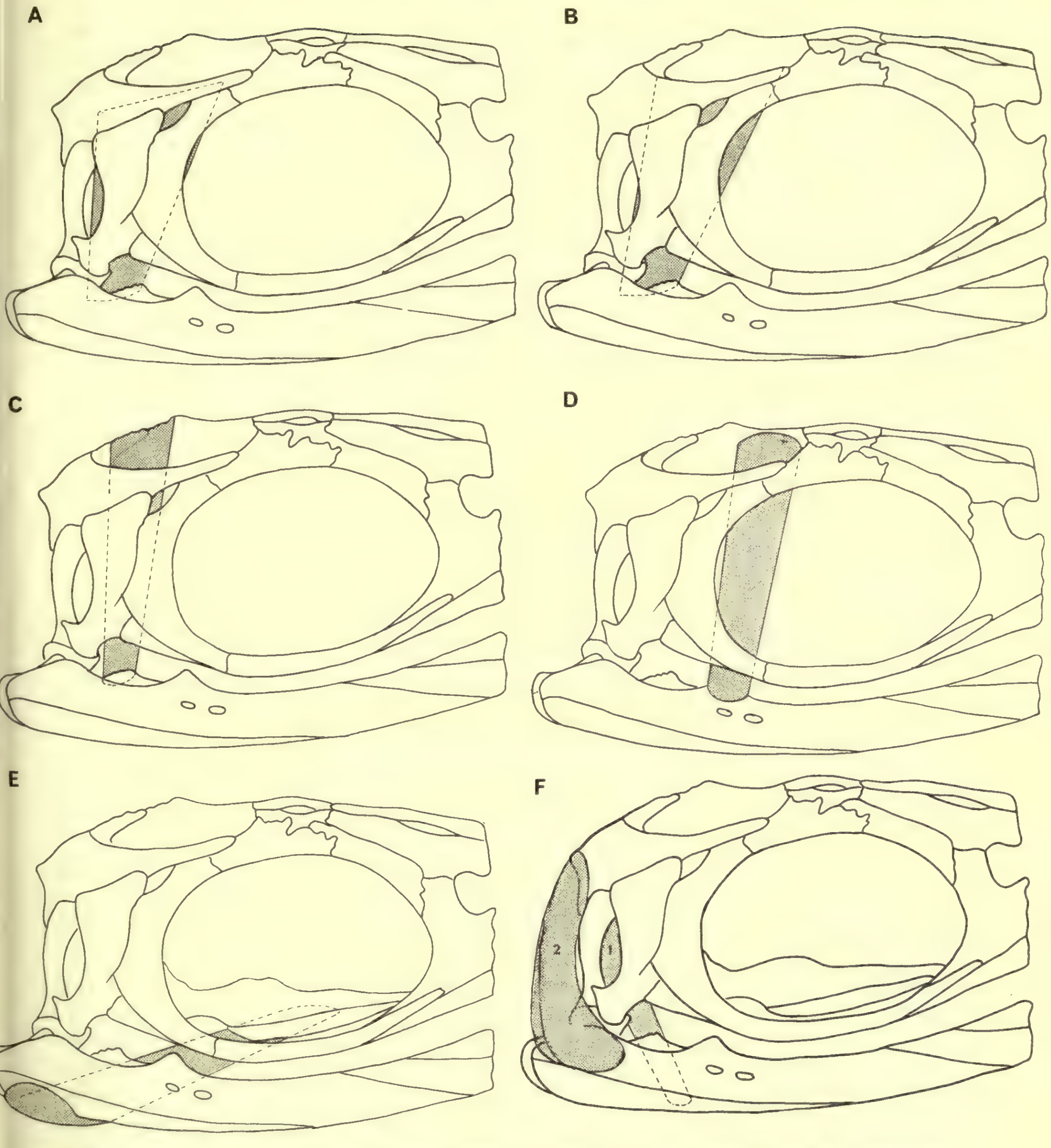

Fig. 51. (a). Lateral view of skull (R8177) with a reconstruction of the *M. adductor mandibulae externus superficialis* × 1/3. (b). Lateral view of skull (R8177) with a reconstruction of the *M. adductor mandibulae externus medialis* × 1/3. (c). Lateral view of skull (R8177) with a reconstruction of the *M. adductor mandibulae externus profundus* × 1/3. (d). Lateral view of skull (R8177) with a reconstruction of the *M. adductor mandibulae internus pseudotemporalis* × 1/3. (e). Lateral view of skull (R8177) with a reconstruction of the *M. adductor mandibulae internus pterygoideus* × 1/3. (f). Lateral view of skull (R8177) with a reconstruction of 1, the *M. adductor mandibulae posterior*. 2, *M. depressor mandibulae*.

mens (R6697, R8177, Evans' nodule), there is a reticular area in the middle region towards the outer edge which may be the origin of the muscle (fig. 9a).

The abductor muscle (fig. 51f). The reptilian abductor muscle, the *M. depressor mandibulae,* belongs to the branchial group and usually takes origin from the dorsal occipital region to insert on the retroarticular process. The posterior surface of the squamosal is marked by striations which converge upon a backwardly directed bony protuberance, and this is believed to be the origin of the depressor muscle.

When the structure of the jaw was discussed it was noted that the largest muscle insertion area was on the external surface of the surangular (see fig. 25a) and that this has been interpreted as being that for the depressor muscle. When the jaw is articulated this insertion area is largely retroarticular in position. Quite frequently a backward prolongation of the angular is encountered which increases the extent of the retroarticular insertion area but unfortunately the terminal portion of the mandible is often damaged, as in the case of the available prepared material, and it cannot be known with certainty whether it is a constant feature.

FUNCTIONAL MORPHOLOGY AND PHYSIOLOGY

Jaw function

Before discussing jaw function it is necessary to define some mechanical terms in the context in which they are used here.

Moment arm = Perpendicular distance from the pivot to the line of action of the muscle.

$$\text{Mechanical advantage} = \frac{\text{Distance from pivot to effort}}{\text{Distance from pivot to load}}$$

$$= \frac{\text{Moment arm of muscle}}{\text{Distance from pivot to load}}$$

$$\text{Velocity ratio} = \frac{\text{Distance through which load moves}}{\text{Distance through which effort moves}}$$

The load arbitrarily will be considered to be acting upon the jaw midway along the dental row, a procedure often followed in discussions of jaw function.

The ichthyosaurian jaw is relatively long and the adductor muscle insertion areas lie very close to the joint. The insertion of the *M. adductor mandibularis externus* lies closer to the pivot than that of the *M. adductor mandibularis internus pseudotemporalis,* and the former muscle therefore has the smaller moment arm and mechanical advantage, but larger velocity ratio. The different mechanical characteristics of these two muscles may be evaluated. In specimen 49203 the jaw has a length of 48·5 cm and the distance from the centre of the articular surface of the articular to the middle of the dental row is 28·5 cm. Measuring between perpendiculars, the distance from the articular to the centre of the dorso-medial insertion area of the *externus*, and to the centre of the coronoid insertion area of the *pseudotemporalis*, are 2·5 and 5·5 cm respectively, (fig. 52a). From this information the following may be evaluated:

Moment arm of *externus* = 2·5
Moment arm of *pseudotemporalis* = 5·5

Mechanical advantage of *externus* $= \frac{2{\cdot}5}{28{\cdot}5} = {\cdot}088$

Mechanical advantage of *pseudotemporalis* $= \frac{5{\cdot}5}{28{\cdot}5} = {\cdot}193$

Velocity ratio of *externus* $= \frac{L}{x}$ (Fig. 52b)

Velocity ratio of *pseudotemporalis* $= \frac{L}{y}$

$x : y : L = 2{\cdot}5 : 5{\cdot}5 : 28{\cdot}5$

$\therefore \frac{y}{x} = \frac{5{\cdot}5}{2{\cdot}5}, \frac{L}{x} = \frac{28{\cdot}5}{2{\cdot}5}$

If $x = 1$, $y = \frac{5{\cdot}5}{2{\cdot}5} = 2{\cdot}2$, $L = \frac{28{\cdot}5}{2{\cdot}5} = 11{\cdot}4$

Velocity ratio of *externus* $= \frac{L}{x} = \frac{11{\cdot}4}{1} = 11{\cdot}4$

Velocity ratio of pseudotemporalis $= \frac{L}{y} = \frac{11{\cdot}4}{2{\cdot}2} = 5{\cdot}2$

From this it can be seen that the mechanical advantage of the *externus* is about half that of the *pseudotemporalis*, while its velocity ratio is approximately double. It may be inferred that while the *externus* provided for rapid adduction, the *pseudotemporalis* contributed much of the power.

During contraction a muscle generally shortens by something like 1/5 to 1/3 of its length (see Smith & Savage, 1956). The lengths of the *externus* and *pseudotemporalis* muscles were similar, and in specimen 49203 were in the order of 9 cm. If these muscles shortened by, say, 1/5 of their length during contraction, the vertical movement brought about in the jaw at the level of the insertion would be about 2 cm. A movement of 2 cm in the *pseudotemporalis* would bring about a movement at the tip of the jaws of about 17 cm. When the abductor muscle is considered it will be seen that it could produce a gape at the tip in excess of 20 cm, and this estimate, like that for the *pseudotemporalis*, is conservative. Bearing in mind the short time taken for a muscle to contract it can be seen that the jaws could be snapped tight upon a suitable prey with great speed.

The line of action of the *M. adductor mandibularis posterior* laid at about 45° to the perpendicular and its insertion was not very far in front of the jaw joint, (fig. 52c). The mechanical advantage was therefore small and it is thought that this muscle contributed a relatively slow but powerful adductor force. This muscle may well have been extensive, filling much of the Meckelian fossa.

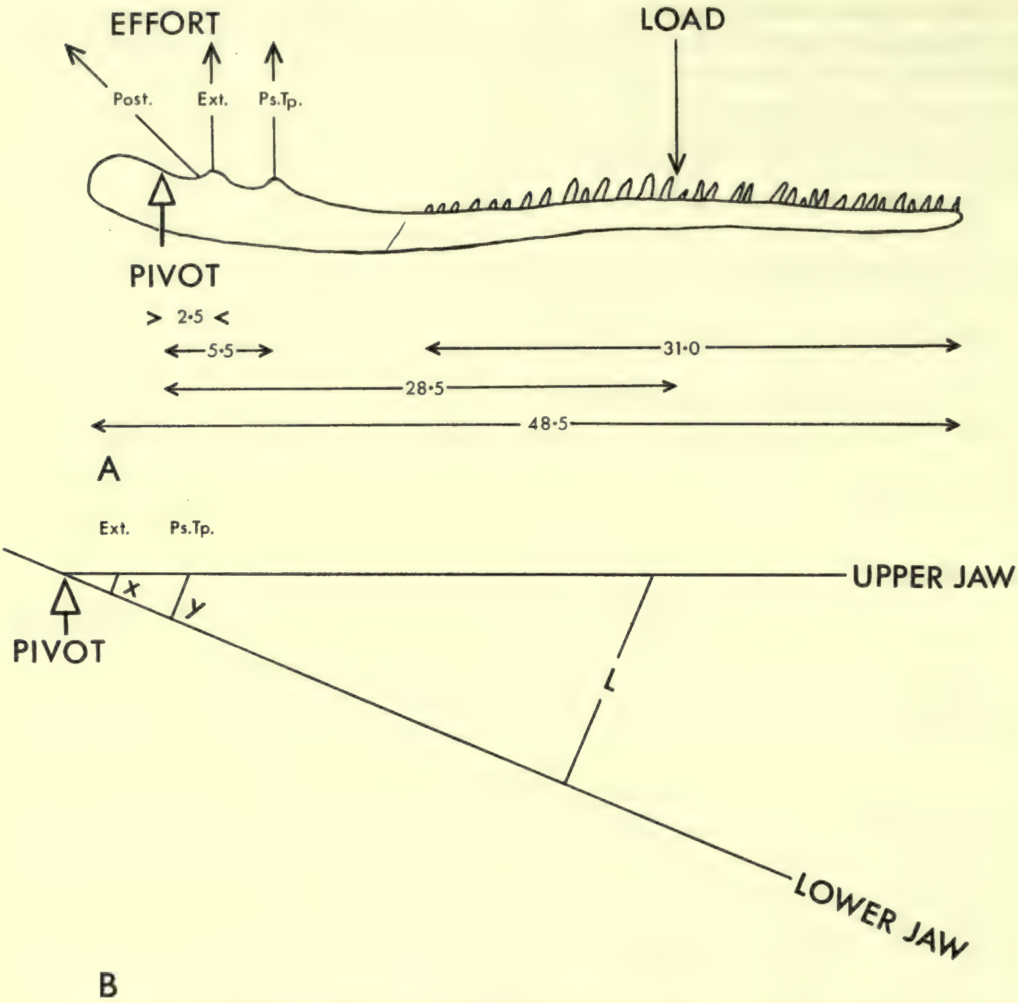

FIG. 52. Jaw mechanics, based upon data from specimen 49203. (a). Lower jaw (right side), lateral view, ×¼. Post., effort produced by the *M. adductor mandibularis posterior*. Ext., effort produced by the *M. adductor mandibularis externus*. Ps. Tp., effort produced by the *M. adductor mandibularis internus pseudotemporalis*. (b). Diagram to show relationship between the distances moved through by the *externus and pseudotemporalis* muscles, and by the load. Ext., effort produced by the *M. adductor mandibularis externus*. Ps. Tp., effort produced by the *M. adductor mandibularis internus pseudotemporalis*. (c). Diagram to show the relative small size of the moment arm of the *M. adductor mandibularis posterior*. post., line of action of the *M. adductor mandibularis posterior*. M., moment arm of same. (d). Diagram to show the relative small size of the moment arm of the *pterygoideus* muscle. ptgys., line of action of the *M. adductor mandibularis internus pterygoideus*. M., moment arm of same. (e). Diagram to show the gape produced at the tip of the jaws when the retroarticular process is moved through a distance of 2 cm by the abductor muscle. Abd., line of action of the *M. depressor mandibularis*.

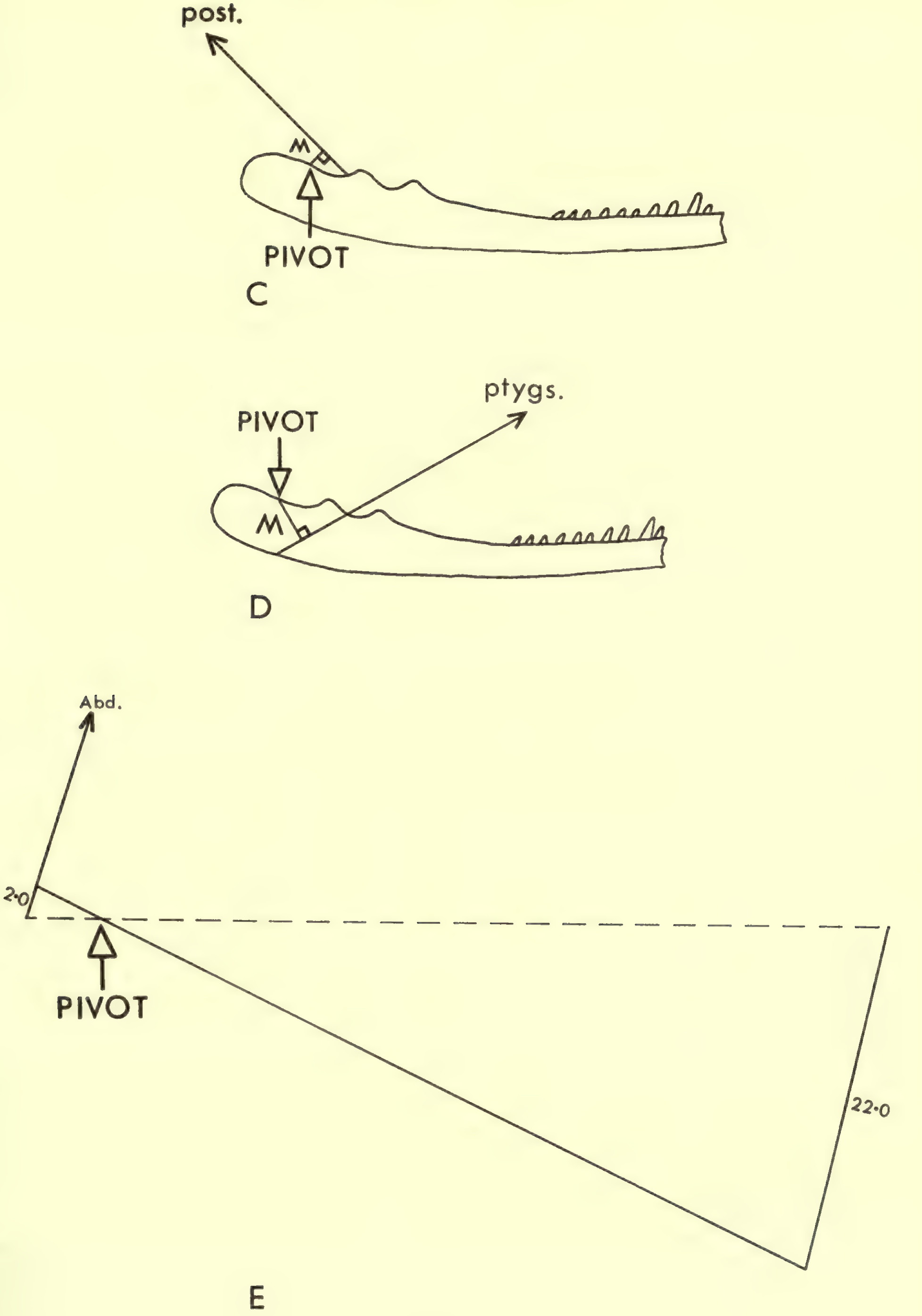
post.
M
PIVOT
C
ptygs.
PIVOT
M
D
Abd.
2·0
PIVOT
22·0
E

FIG. 52

The abductor muscle is somewhat longer than the adductors and in specimen 49203 was in the order of 12 cm. Again, if it is assumed that this muscle shortened by 1/5 its length during contraction, it can be seen that the vertical distance through which the retroarticular process would be moved would be about 2 cm. A movement of this magnitude would produce a gape at the tip of a little more than 22 cm., (fig. 52e).

The upper and lower jaw teeth interdigitate throughout the length of the jaw, as in the Crocodilia and Delphinoidea, and it is essential that there should be no lateral or anteroposterior jaw movements during adduction. Jaw freedom is eliminated in the crocodiles by the descending ectopterygoids, which function as jaw guides, while in the Delphinoidea it is accomplished by the presence of an extensive fibro-connective capsule (Purves, pers. comm.). There are no jaw guides in the ichthyosaurian skull, but the jaw joint is such that the forward and inward facing articular surface of the articular is braced anteriorly against the postero-laterally inclined articular surface of the quadrate. The only displacement permissible is therefore that of an oblique backward shift of the jaw, and this is prevented by the action of the *M. adductor mandibularis internus pterygoideus*. The origin of the *M. adductor mandibularis internus pterygoideus* lies well anterior to its insertion (see fig. 51e), and its line of action subtends an angle of about 30° to the long axis of the jaw. The moment arm of this muscle is therefore short (fig. 52d) and it follows that its mechanical advantage is small. The main function of this muscle was one of pulling the jaw tightly inwards and forwards against the articular surface of the quadrate and it probably contributed but little to the adduction of the jaw. Since the origins of the other adductor muscles were medial and anterior to their insertions, it follows that they also tended to pull the jaw forwards and inwards during adduction assisting the *pterygoideus* in its action. This relationship between the adductor muscles and the jaw joint, together, no doubt, with the presence of an extensive fibrous capsule, served to restrict jaw freedom to the biting plane.

The force exerted by the lower jaw when biting against the upper jaw decreases with distance from the joint, and most of the teeth in the ichthyosaur would have been ineffectual in biting and crushing. This is reflected in the generally slender and pointed form of the teeth, and in the lower jaw's lack of depth. During jaw adduction, which was very rapid, the velocity of the acuminate teeth would enable them to penetrate flesh with ease, especially towards the tip of the snout where the velocity of the teeth was highest. The ichthyosaurian jaw apparatus was therefore an efficient snapping mechanism for the apprehension of fish and other rapid-moving marine organisms.

PHYSIOLOGY

Feeding mechanism

The form of the lower jaw, its musculature, and its dentition, have all the attributes of an animal which fed upon active prey. While the teeth of the upper jaw margin slope posteriorly, those of the lower jaw are inclined forwards, and, when occluded, they interdigitate forming an efficient fish trap. The dentition and jaw proportions are so much like those of *Delphinus* that a similar feeding mechanism is envisaged, but it cannot be concluded that fish alone were taken, and it will be shown below that cephalopods formed a large part of their diet.

In ichthyosaurs and dolphins the buccal cavity is narrow for much of its length, but widens posteriorly. The dolphin feeds by taking one fish at a time which is grasped by the head and swallowed lengthways. Fish of larger size than can be accommodated lengthways in the mouth are probably not taken, maximum size being determined by whether they can be swallowed whole. The teeth therefore serve in the first instance to grasp the fish, then to prevent its escape once within the buccal cavity, they are in no way masticatory. There is no indication of muscle scars on the medial surfaces of the jaw rami marking the position of the muscles of the *constrictor ventralis* group, but this does not necessarily mean that the muscle was not well developed. In many odontocetes these muscles are not well developed and swallowing is probably brought about largely by the tongue. The well developed hyoid arch of the ichthyosaurian skull indicates the possession of a well developed tongue important in swallowing and perhaps also in the manipulation of food.

A preliminary investigation by Pollard (1968) into ichthyosaurian gastric contents has revealed the presence of numerous dibranchiate cephalopod hooklets in a number of specimens, and the remains of fish of the genus *Pholidophorus* in certain others. Pollard examined about twenty specimens in all (pers. comm.), about fifteen of which had recognizable gastric contents. Of these, two possessed remains of *Pholidophorus* (J 13587 and J 13593, both in the Oxford University Museum; the latter also possesses a very sparse scattering of hooklets), while the others had dibranchiate hooklets only.

In addition to examining gastric contents Pollard has made an examination of Lower Liassic coprolites which on faunal, lithological, and chemical grounds he concludes to be identical to the ichthyosaurian gastric contents described by Buckland (1836). Fifty well preserved coprolites were examined from Buckland's Collection in the Oxford University Museum, and forty-five were found to contain recognizable fish remains, largely scales, fin rays, and spines of *Pholidophorus*, less commonly of *Lepidotus* and *Dapedium*. Two more contained reptilian bones, but none contained any visible remains of dibranchiate hooklets. Since hooklets are invariably present in ichthyosaurian gastric contents but absent in (presumed) ichthyosaurian coprolites, it must be concluded that either: (1) Ichthyosaurs had a mixed diet of fishes and cephalopods and that the undigested hooklets were retained in the stomach, or, (2) Some ichthyosaurs lived mainly on fish whilst others lived mainly on cephalopods and only the faeces of the piscivorous forms have been preserved. The latter alternative is most unlikely since there is no reason to suppose that faeces predominating in hooklets are less readily fossilised than those containing only fish remains. Furthermore the presence of hooklets in gastric contents are not restricted to any one species but have been identified in three of the four latipinnate species, *I. conybeari*, *I. breviceps*, and *I. communis* (specimens 38523, 43006 and 36256 respectively). Specimen J13587, one of the two which have fish remains in the gastric contents, is identified as belonging to the species *I. communis*, and it is therefore almost certain that latipinnate ichthyosaurs had a mixed diet comprising of both fishes and cephalopods. While fish scales and spines were egested, cephalopod hooklets were retained in the stomach. A similar circumstance is observed in living sperm whales where squid beaks and other hard parts are retained in the stomach, presumably to avoid damage to the more delicate lining of the intestine. The majority of piscine remains found in coprolites and gastric contents belong, as already noted, to *Pholidophorus*, which was of the order of size of a herring and one of the swiftest of Liassic fishes.

Fish and cephalopods were almost certainly located by sight, but the lack of a binocular vision would have made the judgement of distances difficult. Many of the Osteichthyes have large eyes and correspondingly large optic lobes, but very few have a binocular vision. To what extent a fish uses its eyes in the location of food is not known, but the olfactory organ and the lateral line system are of much significance, (Greenwood, pers. comm.). Perhaps olfaction was important to the ichthyosaur when closing in on its prey, and it has already been noted that olfaction was probably of some importance in the life of the individual. The ear may be dismissed as an organ of location (a discussion of the evidence is given below). Having closed in upon a suitable animal the body was sufficiently agile, and its reactions sufficiently swift, to follow any evasive movements and effect capture. Of cervical vertebrae only the axis and atlas were fused and the cervical count generally exceeds that of the Cetacea. In *I. communis* the mean cervical count is 10 and some individuals possess as many as 12 (specimen R12 in the B.M.N.H.). There were fewer cervicals in the short-snouted species *I. breviceps*, a count of 6 having been made for specimen R216 (B.M.N.H.). Although the 7 cervicals of the dolphin are fused, the head is capable of some degree of movement relative to the body and this is probably of some significance to them during apprehension, and in the manipulation of fish prior to swallowing. From this it may be concluded that the ichthyosaur certainly possessed a greater degree of head mobility than that seen in the dolphin. When the great length of the ichthyosaur's snout is considered it can be appreciated that a relatively small lateral movement of the head would cause the tip of the snout to swing through a considerable arc. In *Xiphius* the great lateral sweeps of the rostrum during hunting are effected, not by movements of the head relative to the body, but by movements of the whole body (Scott, pers. comm.), and there is no reason to suppose that the agile ichthyosaurian body could not similarly implement wide sweeps of the head. The ability to move the head rapidly from side to side has obvious advantages in the seizure of prey. Furthermore some degree of head mobility enables a fish which has been impaled on the teeth to be tossed into a suitable position for swallowing. While an ichthyosaur might have taken most of its fish lengthways so that they could immediately be swallowed, there would have been times when some manipulation would have been necessary. Cephalopods presumably would have needed a good deal of manipulation.

Kinesis

The skulls of many reptiles possess a degree of intra-cranial mobility which assists in the manipulation of captured prey, and in the reduction of stresses on the neurocranium during jaw adduction. Intra-cranial mobility is best exemplified in the Lacertilia (see Robinson, 1967), where the general reduction in ossification has probably been a contributory factor, and at least four forms of mobility have been recognized.

The term kinesis has generally been applied to the mobility of the occipital segment (the cranium) with respect to the maxillary segment (the remainder of the skull). The axis of rotation of the occipital about the maxillary segment is termed the metakinetic axis and lies transversely, passing through the paroccipital process of the opisthotic on either side. The maxillary segment may be divided into two subunits which are moveable upon each other about a second axis, the mesokinetic axis, which is a transverse hinge between the frontals and parietals.

A third form of mobility is that of the quadrate relative to the rest of the skull, termed streptostyl. Skulls may be metakinetic without being streptostylic and vice versa. Lastly, each half of the palate may be capable of movement relative to the rest of the skull by its movement about the basipterygoid-pterygoid joint. Such movements enable the two halves of the palate to be raised and moved forward by the action of muscles of the constrictor dorsalis group (*M. levator pterygoidei* and *M. protractor pterygoidei* respectively), assisting in the retention of a struggling prey. An interesting condition is found in *Sphenodon* (Ostrom, 1962), where in some individuals both the *M. levator pterygoidei* and the *M. protractor pterygoidei* muscles are developed, while in others the muscles are not represented, and this is no doubt correlated with variations in diet.

The ichthyosaurian quadrate could not have been streptostylic because of the firm embrace of its head and much of its leading edge by the squamosal. The oblique slotting union between the parietals and the frontals also removes any possibility of there having been a hinge joint between these two elements. However, the possibility of the existence of mobility between the maxillary and occipital segments, and of mobility of the two halves of the palate relative to the rest of the skull cannot be so readily dismissed. The occipital segment has contact with the maxillary segment at four points:

1. Postero-dorsally between the supraoccipital and the parietal.

2. Postero-laterally between the paroccipital process of the opisthotic and the squamosal.

3. Postero-laterally between the distal facet of the stapes and the stapedial facet of the quadrate.

4. Ventro-medially between the basipterygoid process of the basisphenoid and the articular facet of the pterygoid.

At none of these points is there fusion, but there is very good indication that the free margin of the suproccipital was continued in cartilage which was in turn continuous with the dermal skull roof, and also that the stapes terminated in a pad of cartilage which lodged in the oval depression of the quadrate. The basipterygoid-pterygoid joint possesses a certain degree of freedom, however, and it is conceivable that movement between the occipital and maxillary segments could have occurred at this point, but, in the light of the above, this now seems unlikely.

Since there is a degree of freedom in the articulation between the pterygoids and the occiput it is possible that the two halves of the palate were capable of movement relative to the rest of the skull. However in order that this could occur it would be necessary that fusion did not occur at any of the points of contact of the palate with the rest of the maxillary segment, and of these there are three:

1. Postero-medially between the quadrate wing of the pterygoid and the quadrate.

2. Laterally between the labial margin of the palatine and the medial margin of the maxilla.

3. Postero-dorsally between the foot of the epipterygoid and the groove for its reception on the pterygoid.

The contact surfaces of the quadrate and quadrate wing of the pterygoid are both quite smooth, but it is difficult to see how the pterygoid could have moved relative to the quadrate since its freedom is restricted by its contacts with the basisphenoid, basioccipital and with the squamosal. The palatine meets the maxilla in a well defined and carinate articulation which on initial inspection appears to be modified for movement. However the free edges of the two elements are emarginated, and these emarginations correspond with one another and almost certainly transmitted blood vessels. Clearly no movement between the two elements was permissible. The foot of the epipterygoid rests loosely within the groove on the pterygoid, and movement at this point would seem possible, but it is almost certain that the groove was filled with the cartilaginous vestiges of the palatoquadrate.

That there is no evidence of the origins of muscles of the constrictor dorsalis group is a reflection of the lack of ossification in the otic region, and not necessarily of their absence. The bony pterygoid flange which overhangs the basipterygoid fossa has a rugose margin and could conceivably mark the insertion of the *M. levator pterygoidei*.

From the evidence available at present it is concluded that the ichthyosaurian skull was probably akinetic. While it is recognized that kinetism might have assisted in the manipulation of fish within the buccal cavity, it is noted that no such mechanism exists in dolphins.

External respiration

Before discussing external respiration it is necessary to consider very briefly the habits of ichthyosaurs since this has an important bearing upon the interpretation of the morphological evidence. Were they very active animals which spent most of their time submerged, like cetaceans, surfacing for only brief periods to respire, or were they more akin to their reptilian class in spending most of their time in relative inactivity, diving only periodically for food? This question cannot be answered until an extensive investigation of the post-cranial skeleton has been carried out, but at this stage it would seem that the latter possibility is probably closest to the truth. The main reason for arriving at this conclusion is that reptiles do not possess a diaphragm and it seems unlikely that the ichthyosaurs were capable of the rapid ventilation seen in the Cetacea, or that they possessed comparable physiological adaptations. Furthermore, sustained activity is not a typically reptilian attribute.

From the general body proportions, (plate 9b), it seems likely that an ichthyosaur would float with much of its head beneath the surface. The external narial aperture is not placed very high on the skull, lying approximately at the level of the sclerotic aperture, and would probably not have been clear of the water. Even if the head were held largely above the surface, the turbulence caused by its forward progression would have resulted in the nares being awash for much of the time and they would almost certainly have been guarded by sphincters. The internal nares lie just posterior to the externals, and are more ventral in position, though above the level of the jaw margins. Whether the jaw margins formed a water-tight seal when the mouth was closed is not known, but there would certainly have been a pharyngeal valve at the back of the throat, as in the crocodiles, so that water could not pass from the buccal cavity to the lungs. It seems quite probable that the buccal cavity was water-tight and respiratory exchange could then be effected simply by raising the head and opening the narial sphincter and pharyngeal valve. If on the other hand the buccal cavity were awash while swimming on the surface, it would be necessary to allow the water to drain prior to ventilation. This procedure would be necessary anyway when returning to the surface after diving.

It is rather surprising to find that there was no development of a secondary palate, or any evolutionary tendency for the external nares to migrate to the top of the head, and it is tempting to assign a respiratory function to the median dorsal internasal vacuity which was described above [see footnote]. This aperture is surrounded by a depressed area of bone which could have housed a sphincter, and being high on the head it would always have been kept clear of the water. There may have been a direct air passage connecting this aperture with the pharynx. In life the intrapterygoid vacuity (fig. 38), would have been occupied by the mandibular muscles, but it is just conceivable that the interpterygoid vacuity, even if partly closed by membranes, could have functioned as an internal respiratory aperture (fig. 53). By raising the buccal floor against the buccal roof just in front of these openings, an air passage would be formed enabling respiration to occur with the mouth flooded. However, this is all quite speculative and it may be pointed out that if the internasal aperture were respiratory in function it would provide an unprecedented case of an old structure persisting side by side with a new structure of similar function.

It would be useful to establish the incidence of the internasal foramen in the Lower Liassic latipinnates, but this is not an easy matter. In the first place, because of its median dorsal position, it cannot be demonstrated in laterally exposed specimens and these constitute the majority of ichthyosaurian material. Furthermore, since the foramen lies at the bottom of a shallow depression it cannot be seen if there is any matrix in this region, so that it is almost always necessary to do some preparation on the specimen, which is often not possible. Of the skulls examined during this investigation (see Table 1), the internasal foramen was definitely observed in R8177 and R1168 and seems to have been present in 49203. The other three skulls were incomplete beyond the parietal region. The internasal foramen was present in the skull sectioned by Sollas, and is clearly seen in his sections numbered 359–349 (Sollas 1916 : Fig. 2 (9)).

It is concluded that ventilation probably occurred with the mouth closed and with the head momentarily raised so that the external nares cleared the water. The mouth may well have been water-tight so that ventilation would not always have to be preceded by draining water from the buccal cavity, though this would have been necessary when returning to the surface after a dive.

Olfaction

The olfactory organ of a marine animal is functional only in the detection of water-borne chemostimuli. The external narial aperture of crocodiles and cetaceans has direct communication with the lungs via the nasal canals, and must therefore be closed on submergence, under which conditions the olfactory sense is then lost. In the ichthyosaur, however, in the absence of a secondary palate, the external nares communicated directly with the buccal cavity, and there would be no premium placed upon keeping the external nares closed on diving. It is quite possible therefore that the nares opened on occasion in order to sample the water. Indeed the external nares may have remained open for much of the time so that the water could be continuously sampled.

It has already been noted in the descriptive section that the vomers were produced dorsally into thin bony lamellae which extended into the nasal passage like mammalian turbinal bones. Since the air over the sea is virtually devoid of particulate matter it is doubtful whether the lamellae supported a mucous-secreting epithelium for filtration, and it seems reasonable that a fairly extensive olfactory epithelium was present. The olfactory lobes of the brain were not particularly large, but were moderately well differentiated, and it would appear that olfaction, although very much subordinate to sight may have been of some significance in the life of the individual.

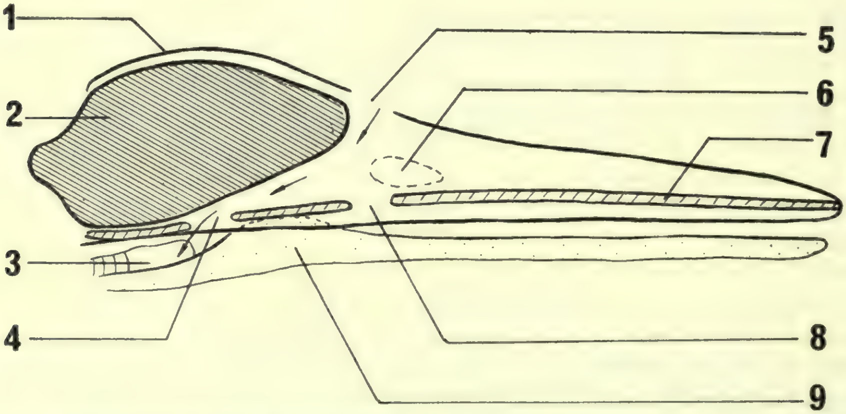

FIG. 53. Longitudinal section through skull showing hypothetical air passage connecting the internasal foramen with the larynx. 1, dermal roof. 2, neurocranium. 3, larynx. 4, interpterygoid vacuity. 5, internasal foramen. 6, external narial aperture. 7, palate. 8, internal narial aperture. 9, tongue.

Hearing

The whole problem of a directional hearing underwater is perplexing and one on which specialists are a long way from reaching agreement. The following discussion, therefore, cannot claim to be on a particularly firm footing. However, it is hoped that it will demonstrate that the possession of directional hearing by the ichthyosaurs is extremely doubtful.

The detection by a terrestrial animal of the direction of a sound source depends partly upon the arrival of vibrations at the two receptor organs at slightly different times. The density of animal tissue differs so much from that of the surrounding air that very little absorption occurs, and the sound waves impinging on the head are largely reflected. Only those vibrations falling upon the pinna reach the inner ear, and conduction through bone does not occur to any extent. In aquatic animals, however, the situation is reversed because the density of the water does not differ very much from that of the body tissues. Incident vibrations are conducted through the body, largely through bone, rather than being reflected. Since the velocity of sound in bone is high, and the distance between the two inner ear structures is relatively small, sound waves reaching the receptor farther from the source, by conduction through bone, arrive at virtually the same instant as those reaching the other receptor, and great difficulty is experienced in locating the sound source.

The cetacean ear, however, is a very sensitive apparatus which can accurately determine the direction of a sound source, and it is able to do this partly because each otic capsule is insulated from the rest of the skull by adipose and vascular tissue. Only those vibrations passing down the external auditory meatus reach the cochlea, and there is consequently a significant time lag in the arrival of vibrations at the two receptors (Slijper 1962).

There is evidence to suggest that seals are able to locate sound sources underwater, in spite of the fact that the otic capsule of the seal is firmly attached to the skull. However, it has been pointed out by Reppening (pers. comm.) that the petrosal is fused firmly only with the mastoid, and while the mastoid is fused to the squamosal and bulla, the entire temporal system of ossification is more or less detached or unfused with other bones of the skull. There is thus some measure of bony discontinuity, most conspicuous in the basioccipital region. Sound entering the head from one side has to pass across several bone/flesh reflective surfaces before reaching the cochlea of the other side. There would, then, seem to be some measure of isolation of the otic capsules in the seal. Furthermore, the high density of the bone of the bulla is probably of great significance in reflecting much of the sound falling upon it.

A further problem facing aquatic animals is that of the hydrostatic pressure upon the tympanic membrane. The cetaceans have evolved a compensatory mechanism whereby the pressure within the tympanic cavity is increased on diving; this equalises the pressure on either side of the membrane, thus preventing its rupture and permitting it to oscillate freely. The oscillations of the tympanic membrane are conducted to the fenestra ovalis by the otic ossicles which, therefore, must clearly be free to vibrate.

The remarkable accuracy of the cetacean location system is inherent in the use of high-frequency emissions which give a better resolution than low frequencies. Clearly the ability to perceive high-frequency sounds is dependent upon the possession of a fairly sophisticated sensory receptor.

At this point it would be useful to list the apparent requirements for directional hearing underwater:

1. Some measure of isolation of the otic capsule.
2. A mechanism for equalising the pressure on either side of the typanic membrane.
3. Freely oscillating otic ossicles.
4. Sensory receptors which are sensitive to high frequencies.

The ichthyosaurian otic capsule is firmly braced against the squamosal, basioccipital and stapes, and there could be no flesh-bone interfaces at any of these points. There was, however, some cartilage in the otic region, and at least at the basioccipital contact there was an intervening pad of cartilage. It would therefore appear that the two capsules had a good degree of direct bony contact with one another.

The stapes is firmly wedged between the basioccipital and opisthotic proximally, and the quadrate distally, so that any oscillation of the stapes must be denied. If the stapes were not free to oscillate it could not have served to transmit vibrations from the tympanic membrane to the fenestra ovalis. Furthermore the evolution of some pressure equalisation system for the tympanum, comparable to that seen in the Cetacea, does seem a little unlikely. In the absence of evidence to the contrary it is concluded that the tympanic membrane had probably been lost altogether.

The last piece of evidence to support the absence of direction location in the ichthyosaurs is the nature of the sensory receptor. It has already been noted (p. 75) that the lagena was probably a small structure, and this evidence, slender as it might be, is not suggestive of an acute sense of hearing. Furthermore, as far as the author is aware, high-frequency response is not an attribute of the reptilian ear. It is therefore concluded that the possession of directional hearing capabilities in the ichthyosaurs is extremely doubtful.

Sight

That ichthyosaurs lived in neritic waters is evident from the associated fauna which contains some terrestrial organisms. Since the silt deposited was very fine it is apparent that these were still waters, where light intensities were probably relatively high. The large size of the orbit, sclerotic ring, and optic lobe of the brain corroborates the importance of sight in ichthyosaurs. In those latipinnates which have been examined, the aperture of the sclerotic ring is relatively large and circumscribed by a shallow sulcus. In terrestrial reptiles the cornea is an important refracting body, and its outer convexity is maintained by a prominent sclerotic sulcus (fig. 54). In aquatic animals the difference in refractive index between the corneal tissue, with its underlying aqueous humour, and the surrounding water is so small that the cornea is no longer functional as a refracting body and is very much reduced. In consequence the sclerotic ring of an animal which uses its eyes primarily underwater has little or no development of a sulcus, and intermediate conditions are found in those forms which use their eyes partly above water, (Underwood, pers. comm.). The inference from the material examined is that the ichthyosaurian sclerotic ring did not support a very prominent cornea, and the eye was primarily adapted for underwater vision. This conclusion is supported by the relatively large size of the sclerotic aperture, which is indicative of an eye adapted to operating in dull light.

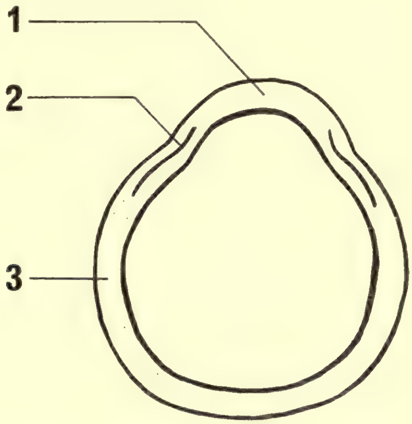

FIG. 54. Sagittal section through the eye of a terrestrial reptile. 1, cornea. 2, sulcus of sclerotic plate. 3, sclerotic layer.

CONCLUSION

The present investigation, it is hoped, will clear up some of the anomalies which have been associated with ichthyosaurian cranial anatomy, and also demonstrate the affinity of the ichthyosaurs with the euryapsid reptiles. It is regretted that so much of this work had to be devoted to straightforward description, which is not absorbing reading, but a detailed account of the skull has been long overdue. The morphological treatment, however, has permitted certain conclusions to be drawn concerning the way these animals lived, and any information which adds to a picture of Mesozoic life justifies the efforts involved.

The ichthyosaur may be visualized as a highly successful animal whose adaptations to a life at sea have been surpassed only by the Cetacea, then only after the passage of some considerable interval of time. Some measure of their success is reflected in the wealth of material which they have left behind. Their heyday came during the early part of the Jurassic when they thronged the shallow seas which covered so much of the globe. Well before the close of the Jurassic, however, their numbers began to dwindle, and relatively few survived into the Cretaceous. While the last chapters of the Age of Reptiles were being written on the land, the last of the ichthyosaurs slipped quietly and unpretentiously into oblivion. Perhaps one day we shall understand why.

TECHNIQUES

The use of 'Carbowax'. 'Carbowax', the water-soluble wax used to cement the elements, is available with a number of different melting points, and that used here, 'Carbowax 4000', melts at about 60°C. If the wax is kept in a boiling water bath it remains mobile, and when applied to the point of contact between two bones it spreads rapidly forming a firm union within seconds. If a less permanent join is required the wax is allowed to cool before application, so that spreading does not occur, and the wax then forms a bead which can subsequently be removed quite easily. This method of cementation was used during the early stages of the reconstruction so that readjustments in orientation could be effected with little difficulty. After a particular section had been completed the joints were made more permanent by remelting the wax with a hot seeker and allowing it to spread between the contact edges. Excess wax may be removed from the surface of bones by using a hot seeker and paper tissue. It must be remembered that skulls which have been reconstructed using wax cannot be left in direct rays of the sun, or anywhere where the wax might soften. Furthermore it has been found that the wax becomes brittle after a month or two and this must be borne in mind when handling a reconstruction which has been stored. The properties of the old wax can be restored by remelting with a hot seeker and allowing it to set, and it is best to do this for each joint before handling stored material. Presumably a slow change in the crystal structure of the wax takes place which reduces its mechanical strength, and this is reversed by remelting.

Sometimes it is necessary to join elements whose area of contact is very small, and this cannot be done in the ordinary way. A technique which has proved very useful is to construct bridging splints of wax and tissue. A piece of tissue is cut to the required size and laid across the gap between the elements to be joined. A drop of hot wax is then applied at either end, and in between. When this is cool, more wax is added, and if greater strength is required more pieces of tissue are

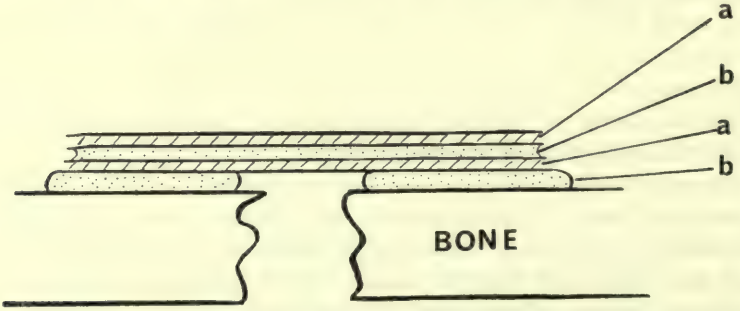

FIG. 55. Section through two bones being temporarily held together by Carbowax tissue bridge. a, tissue. b, Carbowax.

added thus forming a laminated strut (fig. 55). The strut possesses much strength and can readily be removed when it is no longer required. The position of two bones thus joined can be adjusted as desired by warming the strut which becomes plastic and remains pliable for several seconds before cooling to its former rigidity.

A plastic hypodermic syringe was used to deliver the hot wax to the bone, and with a little practice this could be operated orally, leaving both hands free for manipulation.

The most satisfactory method of separating elements affixed with wax is by means of steam delivered in a fine jet. Since some difficulty was initially experienced in obtaining a suitable jet the matter will be discussed here.

The generation of a steam jet. Steam is usually generated in the laboratory by using a steam can. The can is fitted with two exits, one for the delivery of steam, the other serving as a safety valve. The safety outlet comprises a short length of glass tubing which reaches the bottom of the can and extends for several centimetres above the bung. When the pressure within the can exceeds atmospheric pressure a column of water ascends the tube. The effusion of a jet of steam through a fine aperture requires a steam pressure much in excess of atmospheric pressure, and under normal conditions this drives a column of water through the exhaust valve. The apparatus is modified by attaching a long length of rubber tubing to the exhaust and this is held vertically. As the pressure increases water is forced up the tube, but, provided the nozzle aperture is not much less than 2 mm in diameter, the hydrostatic pressure does not exceed about 1 metre. A water-trap is inserted between the steam delivery pipe and the nozzle in order to collect the water carried over with the steam. The steam jet is not required all the time but it is best to keep the water boiling steadily and the steam given off is condensed in the bath in which the wax is kept hot.

In addition to its use in separating wax joints the steam jet is very useful for cleaning bones and has also on many occasions been used for the separation of bones which have been fused together by veins of acid-resistant material. No bone damage has been recorded which is attributable to steaming, and this is mainly because it is localized and does not go on for long periods. Indeed, if pyritic decomposition of fossil bone is brought about by bacterial activity, this technique might have some beneficial effect.

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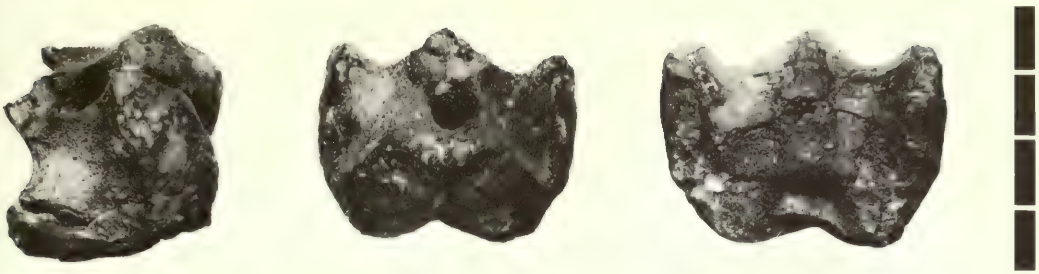
C. McGOWAN, B.Sc., Ph.D.
Dept. of Vertebrate Palaeontology
ROYAL ONTARIO MUSEUM
TORONTO 5
ONTARIO
CANADA

PLATES

Note: Centimetre scale throughout. All specimens referred to are in the collection of the British Museum (Natural History)

PLATE 1

a. Basisphenoid (Evans' nodule), dorsolateral, dorsal and ventral views.
b. Basioccipital (Evans' nodule), dorsolateral, posterior and ventral views.
c. Exoccipital left and right (Evans' nodule), internal, external and dorsal views.
d. Supraoccipital (Evans' nodule), anterior, posterior and ventral views.
e. Opisthotic left (R6697), anterior and posterior views.
f. Proötic, left (Evans' nodule), anterior and posterior views.



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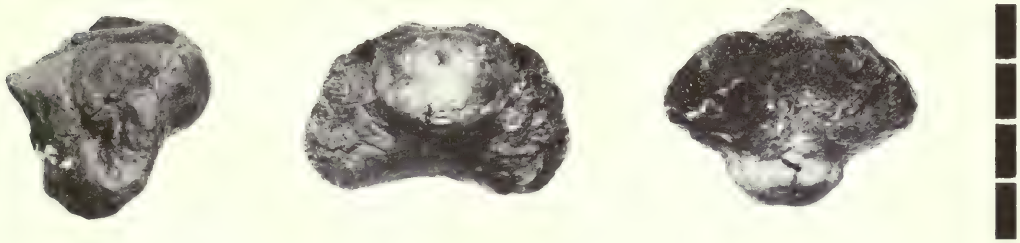

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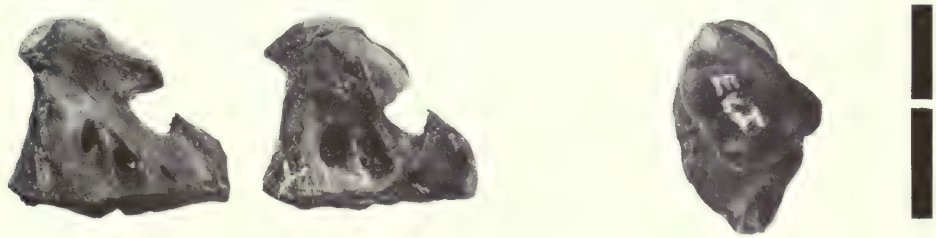

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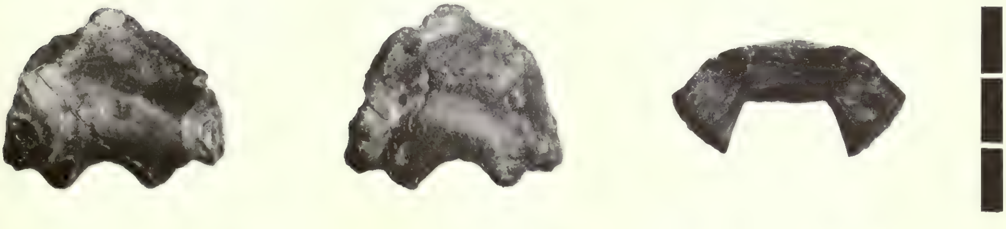

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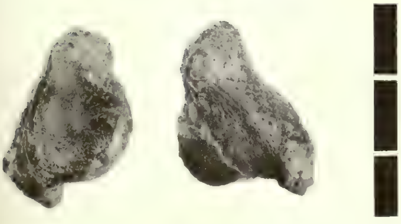

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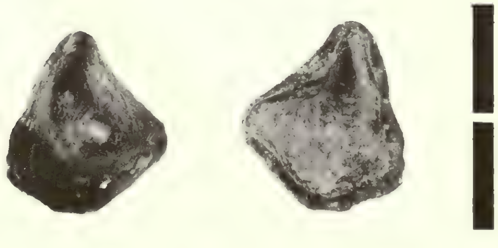

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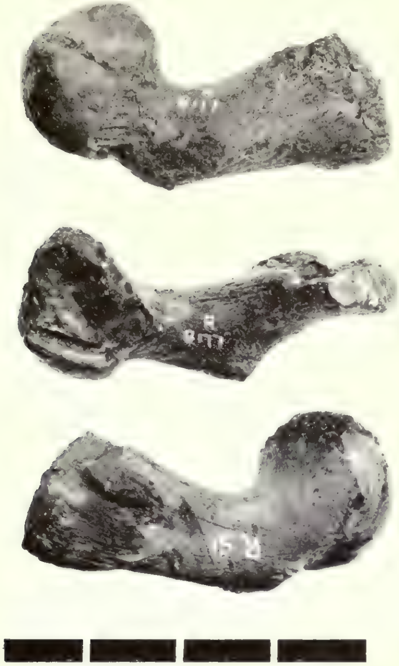
PLATE 2

a. Stapes, right (R8177), posterior, dorsal, and anterior views.
b. Epipterygoid, left (R1168), lateral and medial views.
c. Quadrate, left (R6697), anterior, lateral and posterior views.



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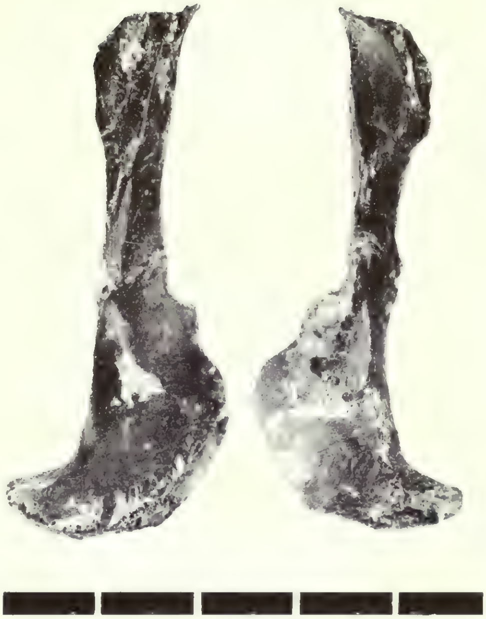

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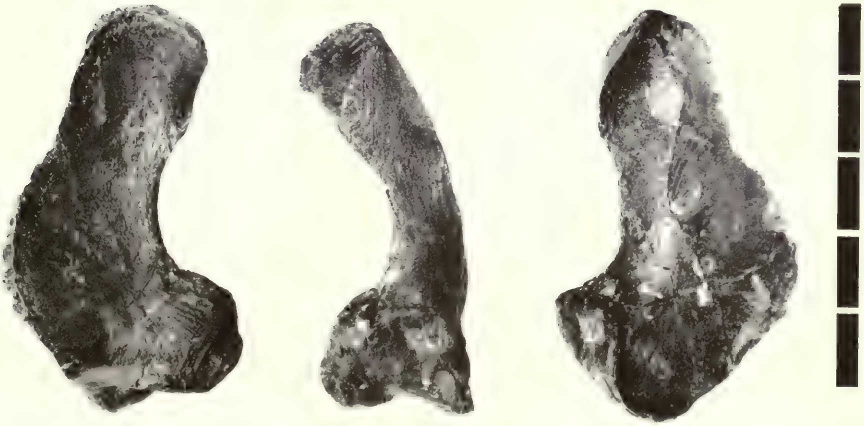

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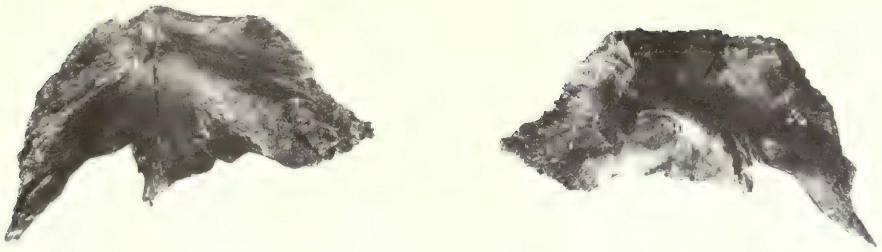
PLATE 3

a. Parietal, right (R8177), dorsolateral and ventral views.
b. Frontal, right (R8177), dorsal and ventral views.
c. Nasal, left (incomplete, posterior portion, R8177), dorsolateral and ventral views.
d. Postfrontal, right (R8177), dorsal and ventral views.
e. Prefrontal, right (R8177), dorsal and ventral views.



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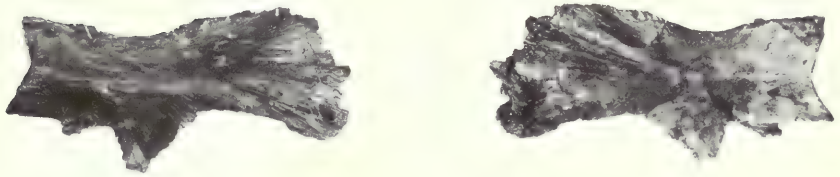

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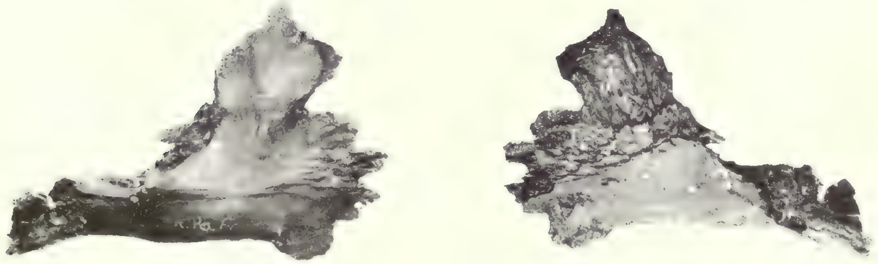

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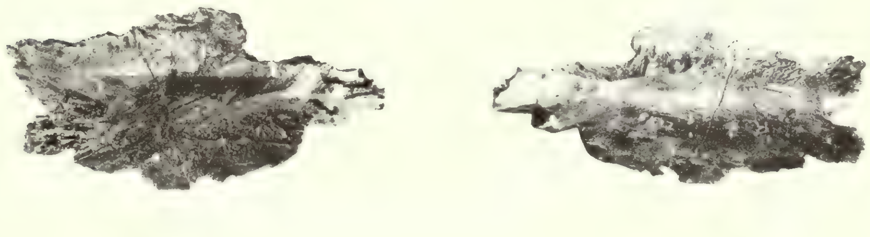

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PLATE 4

a. Postorbital, left (R6697), lateral and medial views.
b. Quadratojugal, right (R6697), posterolateral and internal lateral views.
c. Lachrymal, right (R8177), lateral and medial views.
d. Jugal, right (R8177), lateral and medial views.
e. Maxilla, right (R8177), ventral and dorsal views (incomplete).

PLATE 4

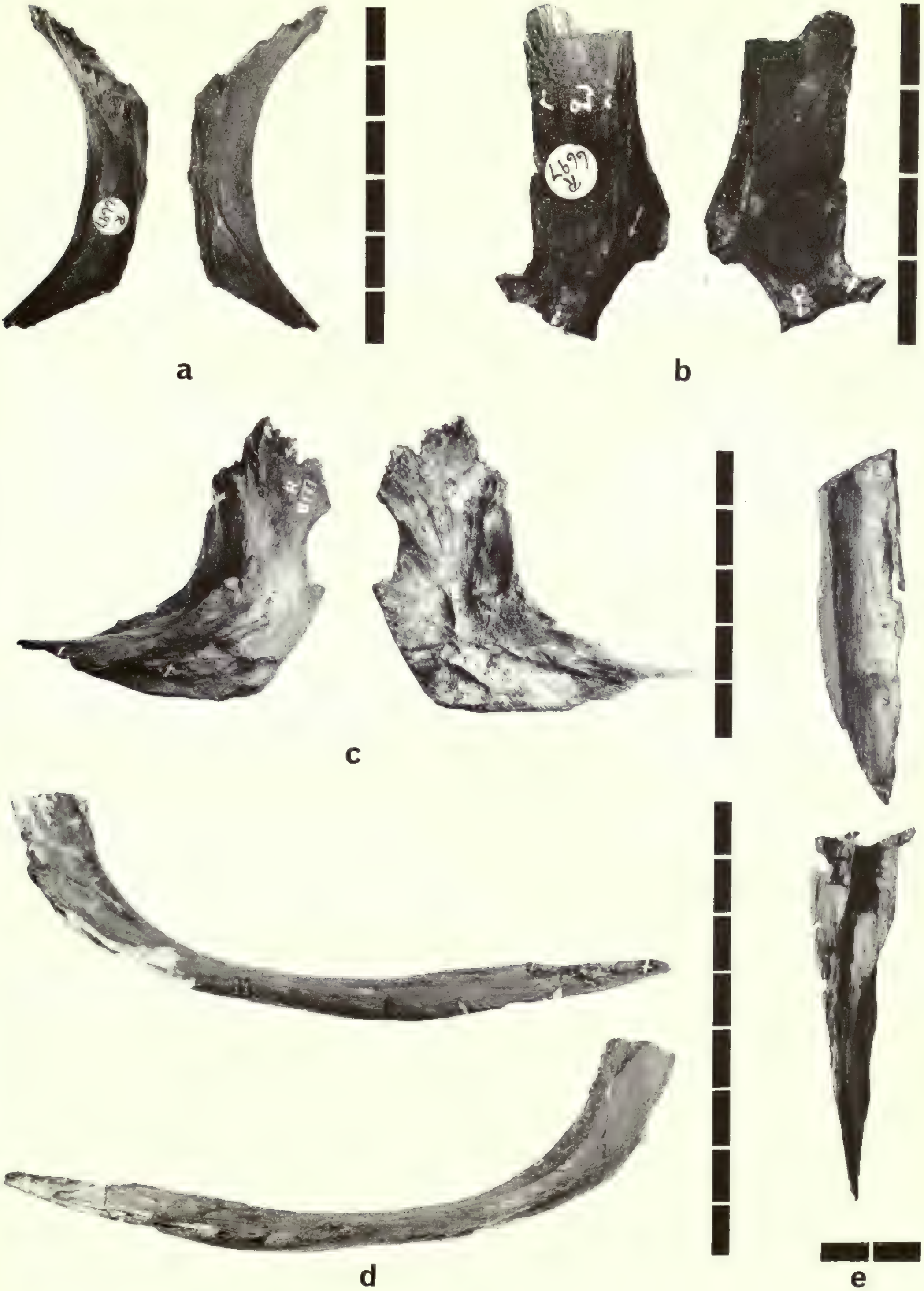
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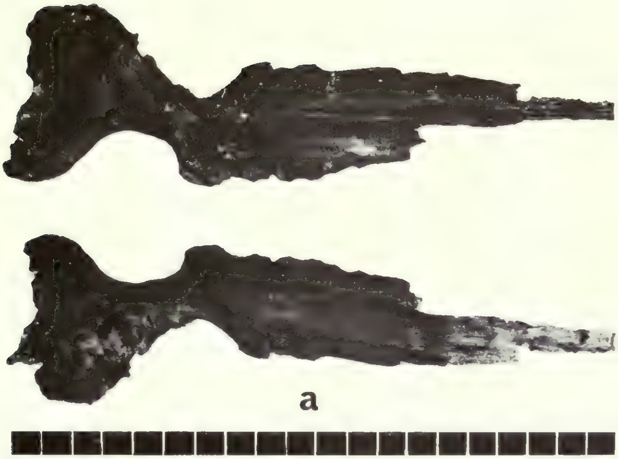
PLATE 5

a. Pterygoid, right (R8177), dorsolateral and ventromedial views.
b. Palatine, left (R8177), dorsal and ventral views.
c. Vomer, right (R8177), dorsolateral, dorsal and ventral views (incomplete).



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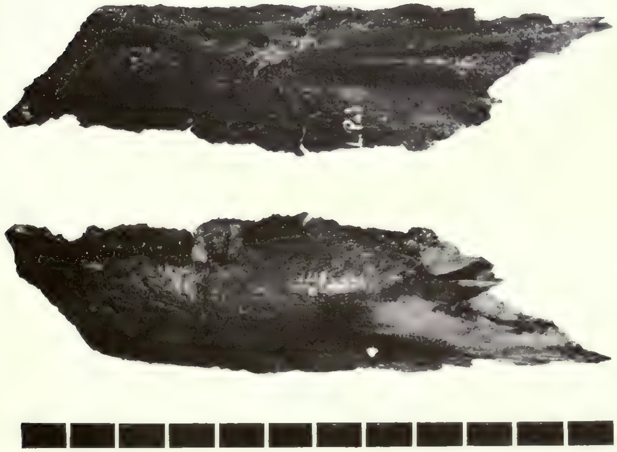

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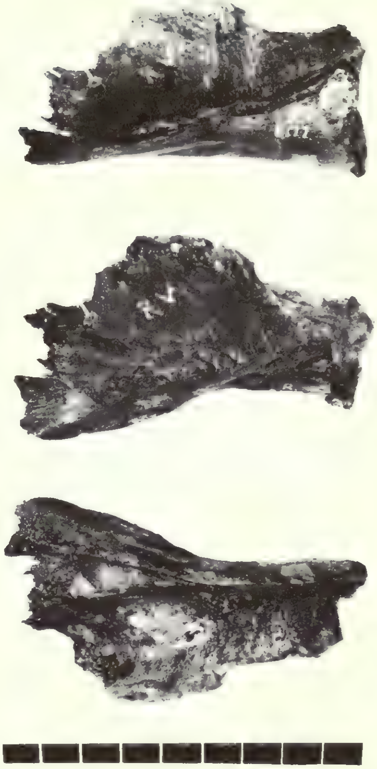

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PLATE 6

a. Lower jaw ramus, right (R8177), lateral, medial, and dorsal views.
b. Prearticular, right (R8177), external and internal views.
c. Coronoid, left (R8177), ventral and dorsal views.
d. Articular, right (R8177), lingual, dorsomedial and labial views.
e. Sclerotic ring, right (half of complete ring, R8177), lateral and medial views.
f. Squamosal, right (R8177), posteromedial and somewhat dorsal, and dorsal views.
g. Teeth in different stages of development (49203).

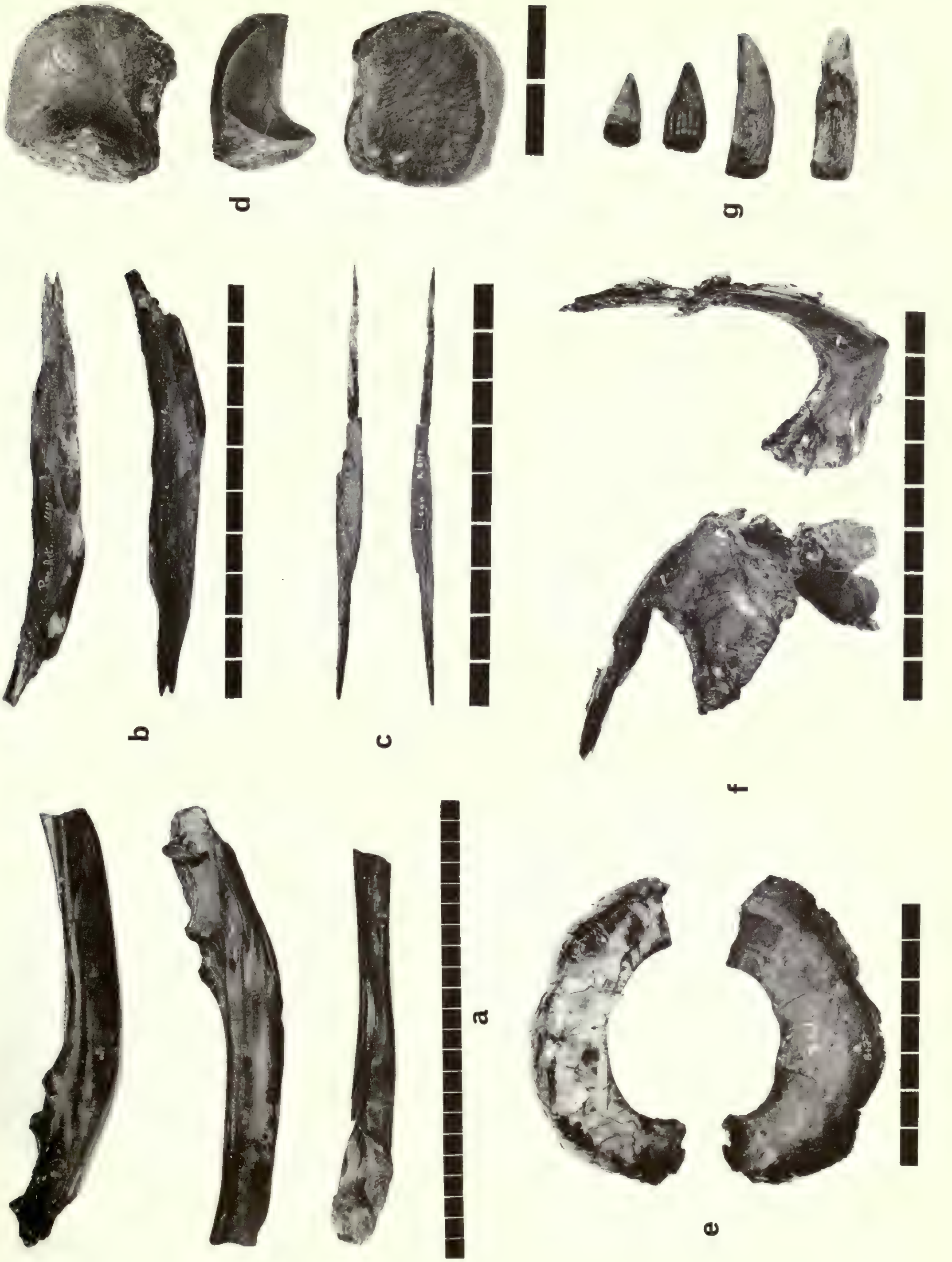
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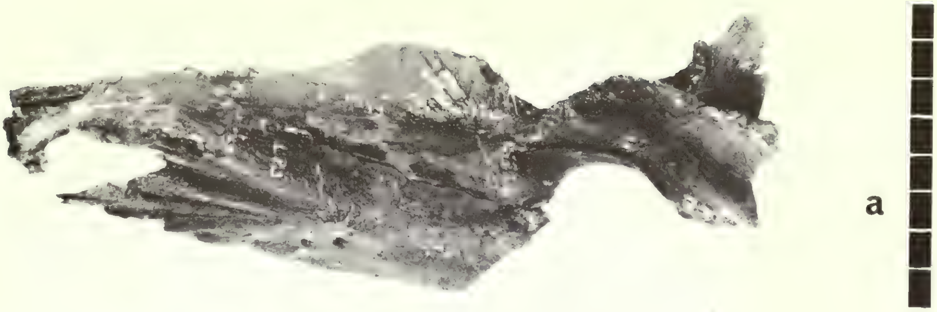
PLATE 7

a. Reconstruction of left half of palate (R8177), dorsal view.
b & c. Partial reconstruction of occiput (Evans' nodule), lateral and anterolateral views.
d. Partial skull reconstruction (R6697), posterior view.
e. Partial skull reconstruction (R8177), complete up to level of external narial aperture, anterolateral and somewhat dorsal view.



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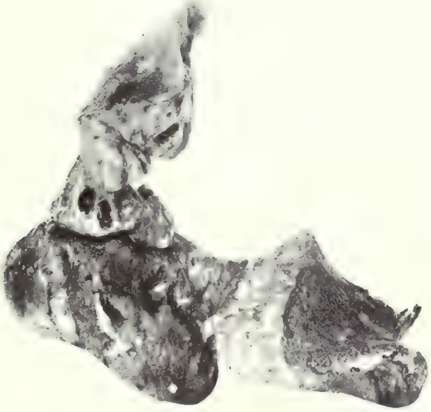

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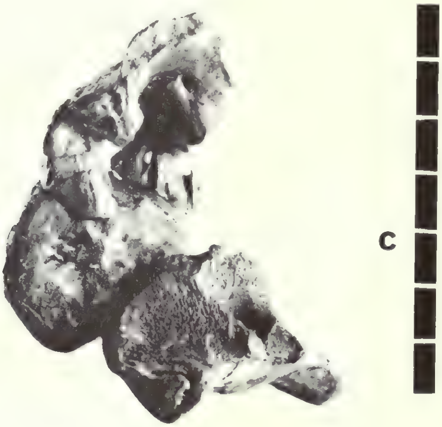

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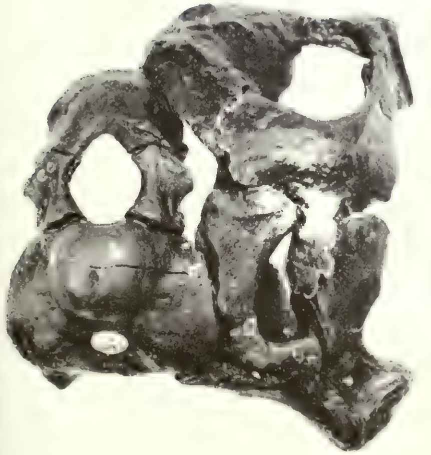

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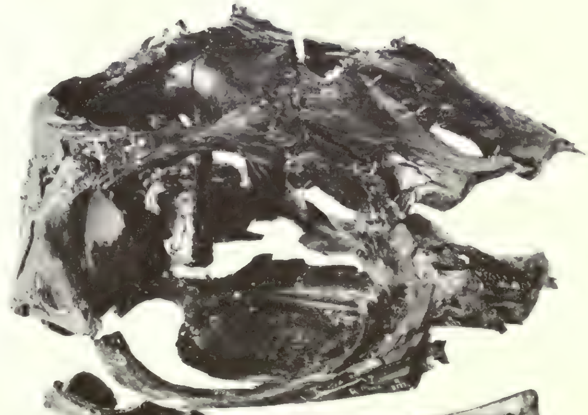

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PLATE 8

a & b. Partial skull reconstruction (R8177), complete up to level of external narial aperture, dorsal and ventral views.

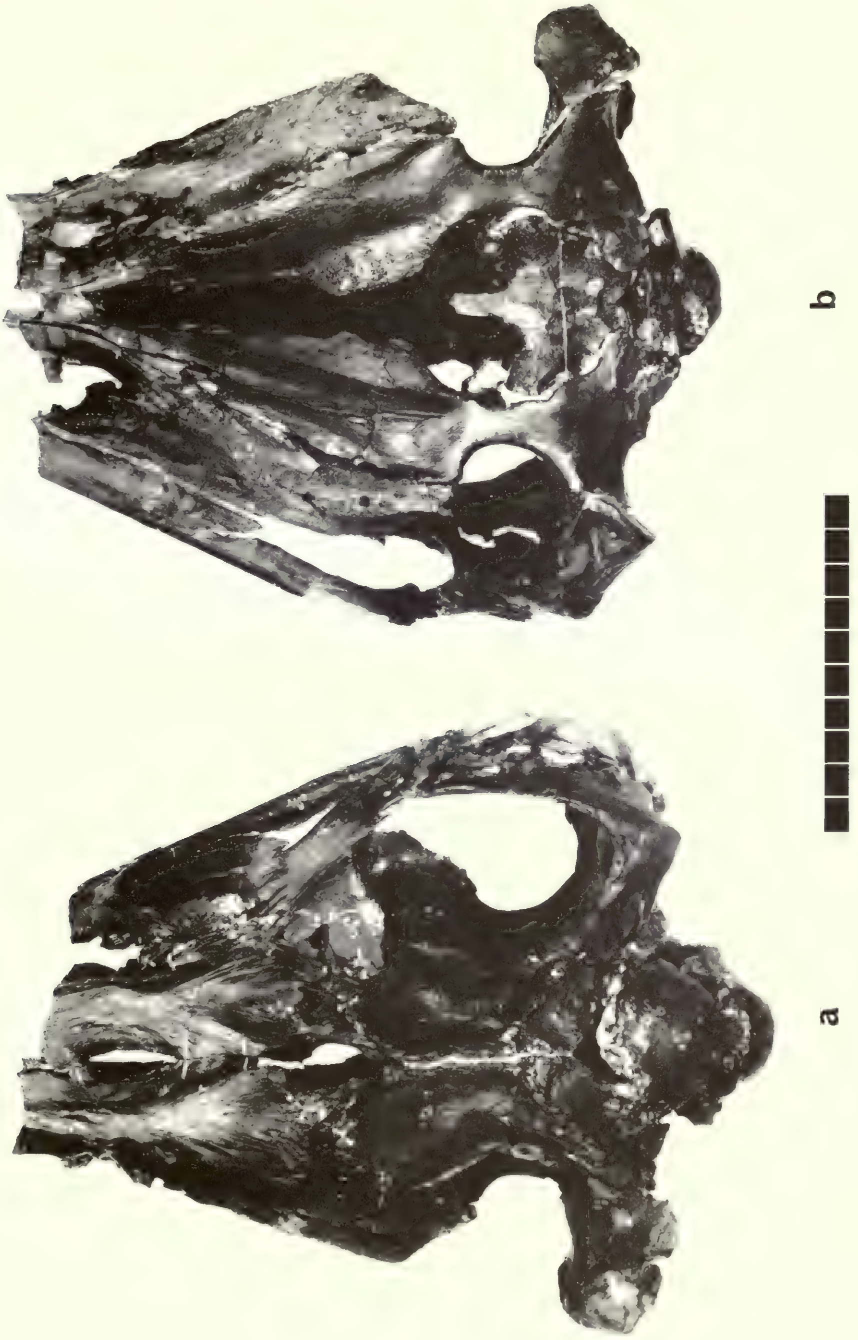
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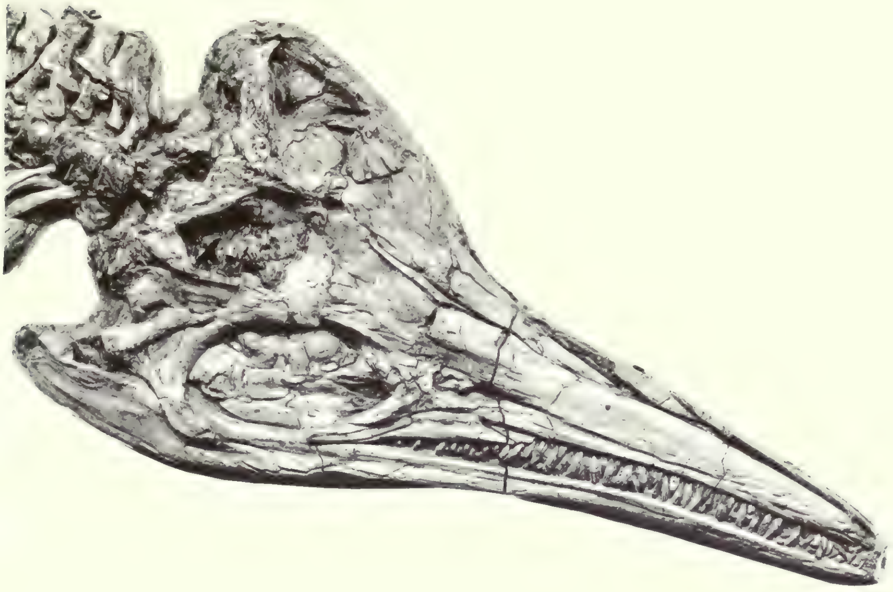
PLATE 9

a. Skull of a well preserved and complete specimen (2013), from the Lower Lias of Street, Somersetshire, dorso-lateral view, about one quarter natural size.

b. Complete skeleton (R4086), showing body outline preserved as a carbonaceous film, from the Upper Lias of Holzmaden, Germany, about one-eleventh natural size.



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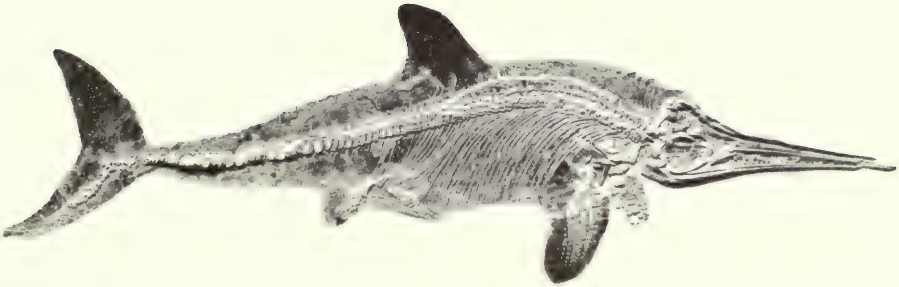

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ARTICULATED ACANTHODIAN FISHES FROM THE OLD RED SANDSTONE OF ENGLAND, WITH A REVIEW OF THE STRUCTURE AND EVOLUTION OF THE ACANTHODIAN SHOULDER-GIRDLE

R. S. MILES

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BY

ROGER S. MILES

Pp. 111-213; 21 *Plates,* 43 *Text-figures*

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By R. S. MILES

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SYNOPSIS

Three species of acanthodians are described from the Ditton Series of Wayne Herbert quarry, SW Herefordshire: the climatiids *Ptomacanthus anglicus* gen. et sp. nov. and *Vernicomacanthus waynensis* gen. et sp. nov., and the ischnacanthid *Uraniacanthus spinosus* gen. et sp. nov. *Climatius uncinatus* Powrie from the Lower Old Red Sandstone of Scotland is made the type of *Vernicomacanthus* gen. nov. The relationships of these species are briefly discussed, and some comments are made on the regional variation in the squamation and the nature of the dentition, particularly in connexion with *P. anglicus*. The head skeleton of *Climatius reticulatus* Agassiz is redescribed to provide a standard of comparison for *P. anglicus*, and Watson's interpretation of the gill-covers is contested.

The shoulder-girdle is described in a range of species covering all families of acanthodians, and where possible the pectoral fin is also described. It is confirmed that the acanthodiforms and ischnacanthiforms lack dermal plates, and in these groups the shoulder-girdle comprises only endoskeletal structures. Advanced forms exhibit a procoracoid separate from the scapulocoracoid, and this condition may be associated with the possession of a mobile pectoral spine. The climatiiforms have both ventral plates and prepectoral-intermediate spines associated with the scapulocoracoid, in addition to the pectoral spine. Primitively the plates form a paired lateral and a median series, and all but the posterior median plate (posterior lorical) are associated with a spine of the prepectoral-intermediate series.

Descriptions are given of the climatiids *Erriwacanthus manbrookensis* sp. nov. from the Downton Series of Worcestershire; *Ptomacanthus* sp. indet 1 from the Ditton Series of Herefordshire; and *Ptomacanthus* sp. indet. 2 from the Dittonian of the Ukraine. *Onchus arcuatus* Agassiz is referred to *Sabrinacanthus* gen. nov., and new shoulder-girdle material of this species is described from the Ditton Series of Gloucester. The Gyracanthidae are re-evaluated and referred to the Climatioidei; they include *Gyracanthus* (the type genus), *Gyracanthides* and *Oracanthus*. *Rhadinacanthus* (Diplacanthidae) is considered to be a valid genus.

The homologies, significance and evolution of the dermal elements in the climatioid shoulder-girdle are discussed. The spines and plates are reduced in divers ways, and a marked contrast in this regard is found between climatioids and diplacanthoids. The evolutionary tendencies in acanthodiforms are related to the development of a mobile pectoral spine, as may also be the case in climatioids. The acanthodiforms and ischnacanthiforms may be more closely related to each other than either group is to the climatiiforms. The scapulocoracoid of acanthodians approaches closely the primitive gnathostome type, and is distinct from that of placoderms. In acanthodiforms, although the scapulocoracoid becomes specialised in relation to the development of a mobile fin-spine, it can still be compared closely with that of primitive actinopterygians. The ventral plates of climatiiforms are not homologous with those of osteichthyans or placoderms. The pectoral fin and its articulation with the girdle may indicate that acanthodians are phylogenetically closer to osteichthyans than they are to chondrichthyans, but the shoulder-girdle yields no decisive evidence on the relationships of acanthodians.

I. INTRODUCTION

THE articulated acanthodians described below were collected by Dr E. I. White and Mr H. A. Toombs in August 1934. The specimens were obtained from the siltstone lenticle that yielded White's (1935) complete specimens of *Pteraspis rostrata* (Agassiz). They have been mentioned in a number of publications (e.g. White 1935 : 383, 1950 : 56; Denison 1956 : 394, 425; Allen & Tarlo 1963 : 145–146), but they have not been described and have unfortunately attracted some misleading taxonomic designations. They are, however, well worthy of description, both for the rarity of articulated acanthodians in Devonian rocks and for their unusually fine preservation. Together with the species from Angus, Scotland, they are the only articulated Lower Devonian acanthodians, and the oldest intact specimens.

The occurrence of the Wayne Herbert fauna has been described by White (1935 : 383). There is general agreement that it comprises fluvial species, trapped by the drying up of the body of water in which they lived.

The specimens have been prepared by etching away the bone with diluted hydrochloric acid, and the resulting moulds have been studied with the aid of rubber casts. The illustration of acanthodians, particularly primitive species in which there are many small bones in the head, has always been difficult. In an effort to maintain a distinction between the specimens (i.e. the evidence) and my interpretations of them, I have attempted in the first part of this paper to illustrate the descriptions mostly with large photographs, accompanied in some cases by key drawings in the text, and then quite separately to summarise the results in restorations. I have selected the shoulder-girdle for special study in the second part of this paper, because it is the only structure found throughout the group in a wide range of species, apart from scales and spines, and thus the only structure likely to throw much light on acanthodian interrelationships. This is not, however, an exhaustive account, and only forms that seemed likely to yield useful results have been studied; no species that deviates markedly from the 'normal' pattern in its family has been deliberately ignored. I believe that a sufficiently wide range of forms has been studied to allow some general conclusions to be drawn. The pectoral fin is less frequently preserved, but where possible it has also been studied.

The following classification is used:

Order ACANTHODIFORMES
  Family **ACANTHODIDAE;** *Acanthodes*
  Family **CHEIRACANTHIDAE;** *Cheiracanthus*
  Family **MESACANTHIDAE;** *Mesacanthus*

Order ISCHNACANTHIFORMES
  Family **ISCHNACANTHIDAE;** *Ischnacanthus, Uraniacanthus* gen. nov.

Order CLIMATIIFORMES
 Suborder CLIMATIOIDEI
  Family **CLIMATIIDAE;** *Brachyacanthus, Climatius, Erriwacanthus, Parexus, Ptomacanthus* gen. nov., *Sabrinacanthus* gen. nov., *Vernicomacanthus* gen. nov.
  Family **EUTHACANTHIDAE;** *Euthacanthus*
  Family **GYRACANTHIDAE;** *Gyracanthus, Gyracanthides, Oracanthus*
 Suborder DIPLACANTHOIDEI
  Family **DIPLACANTHIDAE;** *Diplacanthus, Rhadinacanthus*

Throughout this paper the endoskeletal bones are described as though they are solid structures, although they comprise perichondral bone around a space, originally filled with cartilage and now frequently containing calcite. This infilling is of little interest in the present connexion, and in several species has been adequately described by earlier workers.

Finally the evolution of the shoulder-girdle and the relations of acanthodians are discussed. The main results relate to general evolutionary trends and the interrelations of climatiiforms, but some aspects of the interrelations of the three orders of acanthodians, and the relationships of acanthodians with chondrichthyans and osteichthyans are also considered.

For the loan of specimens I am indebted to Drs S. M. Andrews and C. D. Waterston, Royal Scottish Museum; Dr H. Jaeger, Humboldt University, Berlin; Dr T. Ørvig, Swedish Museum of Natural History; Mr J. M. Edmonds, University Museum, Oxford; and the authorities of the Scottish and London offices of the Institute of Geological Sciences. Miss V. T. Young has assisted estimably with the illustrations, and Drs S. M. Andrews and C. Patterson have kindly read and commented on the manuscript.

The following abbreviations are used: BM, British Museum (Natural History); GSE, Institute of Geological Sciences, Edinburgh; GSM, Institute of Geological Sciences, London; HU, Palaeontological Institute of the Humboldt University, Berlin; RSM, Royal Scottish Museum; SMNH, Swedish Museum of Natural History; UMO, University Museum, Oxford.

II. THE WAYNE HERBERT ACANTHODIANS

Order CLIMATIIFORMES
Suborder CLIMATIOIDEI
Family **CLIMATIIDAE**

PTOMACANTHUS gen. nov.

ETYMOLOGY. Gr. *ptoma*, a corpse; Gr. *akantha*, a thorn.

DEFINITION. Acanthodians with coarsely-ribbed spines; the shoulder-girdle is perichondrally ossified with a broad scapular blade and large coracoid process, and carries paired prepectoral spines 1 and 3; there is a median prepectoral spine; the anterior dorsal fin-spine is curved and not much longer than the posterior, which is almost straight; the body scales each have a moderately high crown with a posterior point and a paired lateral point; the dentition comprises both upper and lower jaw teeth in the form of spirals with several flat, blade-like cusps; there are no dentigerous jaw-bones.

TYPE SPECIES. *Ptomacanthus anglicus* sp. nov.

REMARKS. The terms given to the prepectoral spines are explained in the second part of this paper.

PTOMACANTHUS ANGLICUS sp. nov.

Pl. 1, fig. 2, Pls. 4–6

1950 large Brachyacanthids; White : 56
1961 a large acanthodian; Denison : 181

ETYMOLOGY. From Angle, a member of the Teutonic tribe that settled in England in the 5th Cent A.D.

DEFINITION. A species reaching a length of at least 300 mm; with three pairs of intermediate spines posterior to the shoulder-girdle. This is the only definable species.

TYPE. The holotype is a complete fish in part and counterpart, BM P.19998–9 (Pl. 1, fig. 2).

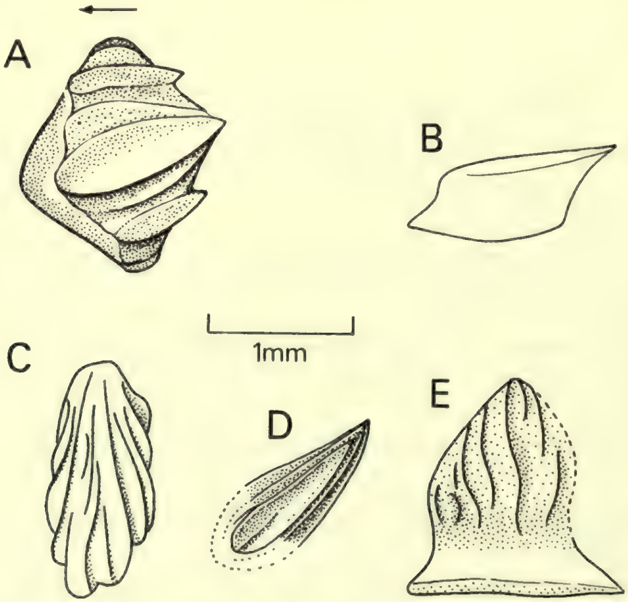
HORIZON. Ditton Series, about 66 m above the main '*Psammosteus*' Limestone, in the *Pteraspis crouchi* zone.

LOCALITY. Wayne Herbert quarry, near Newton, SW. Herefordshire; in the siltstone lenticle described by White (1935 : 383).

MATERIAL. This study is based on six individuals in the BM; P.19998–9, the holotype; P.16615, a large area of squamation from the middle of the body, from which thin sections of the scales have at some time been prepared; P.20002–3, an almost complete fish in part and counterpart but not showing the head and caudal fin well; P.24919a, b, a skull in part and counterpart; P.53037–8, the posterior part of the body as far as the root of the tail, in part and counterpart; P.53285a, b, the left pectoral spine and part of the scapulocoracoid. The thin sections in the collection do not show fine details of structure, and bone histology is not included in this study.

REMARKS. Shoulder-girdles and spines of *Ptomacanthus* are found at other horizons in the English Dittonian and probably belong to a distinct species. They are described in the second part of this paper, together with a shoulder-girdle of *Ptomacanthus* sp. from the Ukraine (pp. 175–176). New species are not named for these specimens as it is impossible to provide satisfactory definitions.

DESCRIPTION. (i) *General features*. *P. anglicus* is a large climatiid with a moderately deep body clothed in thick scales, and with thick tesserae on the skull. The length of the holotype is estimated to be 325 mm. Additional measurements are given in Table 1. The holotype and other articulated specimens are laterally compressed, but in P.20002–3 the ventral region of the shoulder-girdle and the body wall between the intermediate spines have been turned in the same plane as the flank. This suggests a moderately deep body with a broad venter. The detached head, P.24919a, b, is dorsoventrally compressed and this indicates that the skull-



TEXT-FIG. 1. *Ptomacanthus anglicus* gen. et sp. nov. Lower Old Red Sandstone. A, crown of dorsal flank scale; B, side profile of flank scale; C, crown of scale from lateral surface of scapular blade; D, crown of scale from web of posterior dorsal fin; E, lateral view of scale from ventral surface of shoulder-girdle. A, B, D after holotype, BM P.19998–9; C, E after BM P.20003. Ditton series, Wayne Herbert quarry, Newton, Herefordshire, England.

TABLE 1

Length (in millimetres) of exserted portion of fin-spines of *Ptomacanthus anglicus* gen. et sp. nov. measured in a straight line from the middle of the base line to the tip.

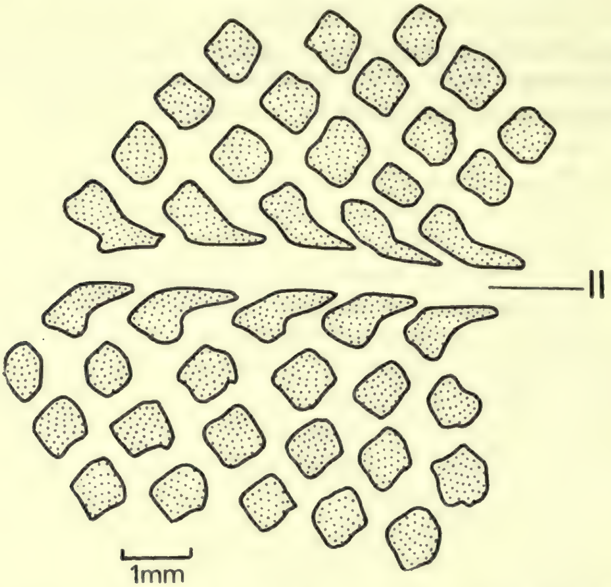
Specimen	Ant. dorsal	Post. dorsal	Pectoral	Pelvic	Anal
P.19998–9	40	35	—	Ca. 24	38
P.20002–3	30	28	Ca. 35	20	Ca. 28
P.53037–8	—	—	—	—	41
P.53285a, b	—	—	Ca. 50	—	—

roof was broad. The eyes were large, as in other acanthodians, and the snout is short and blunt. The fin-spines are placed much as they are in *Climatius reticulatus* Agassiz, with the anterior dorsal inserted posterior to the base of the pectoral and the posterior dorsal situated between the transverse levels of the pelvics and anal. None of the spines is unduly lengthened.

(ii) *Squamation.* The scales of the flank are of a uniform basic type. They have a moderately high crown, which is terraced at either side of a navicular central area which projects posteriorly to a distinct point (Text-fig. 1A). A lateral navicular area may also project back to a posterior point at either side of the central area. Generally the central area is slightly depressed, but it may be flat, and in some cases it bears a slight median ridge. The development of the lateral posterior points also varies, but apparently in a random way over the flank. In some scales they are prominently formed and in others barely distinguishable. Dorsally on the flank the crowns are directed posterodorsally, but lower down their orientation gradually changes so that at the level of the horizontal septum they are horizontally placed, and in the lower part of the flank they become posteroventrally directed. Over most of the body the scales are of almost uniform size, with, e.g., the length of the crown rarely much above 1 mm in the holotype; but they are enlarged ventrally behind the shoulder-girdle in the body cavity region, and in the holotype the crowns here reach a length of about 2 mm. The bases of the scales are slightly swollen (Text-fig. 1B), and in ventral view show typical concentric growth lines. At either side of the main lateral-line the bases of the scales are drawn out to border the course of the line (Text-fig. 2), but on present evidence it is not possible to say whether they are extended in the anterior or posterior direction.

A distinctive type of scale is found in the shoulder-girdle region. On the lateral face of the scapular blade, to which the scale bases are closely applied, the crowns are broad and flat, and ornamented with narrow ridges (Text-fig. 1C). It appears that the terracing of the scales has been destroyed by their flattening, in comparison with normal flank scales. In contrast to this, on the ventral surface below the coracoid and coracoid process, the scales crowns are high and laterally compressed, although again they are ornamented with narrow ridges and have a thin, flat base (Text-fig. 1E).

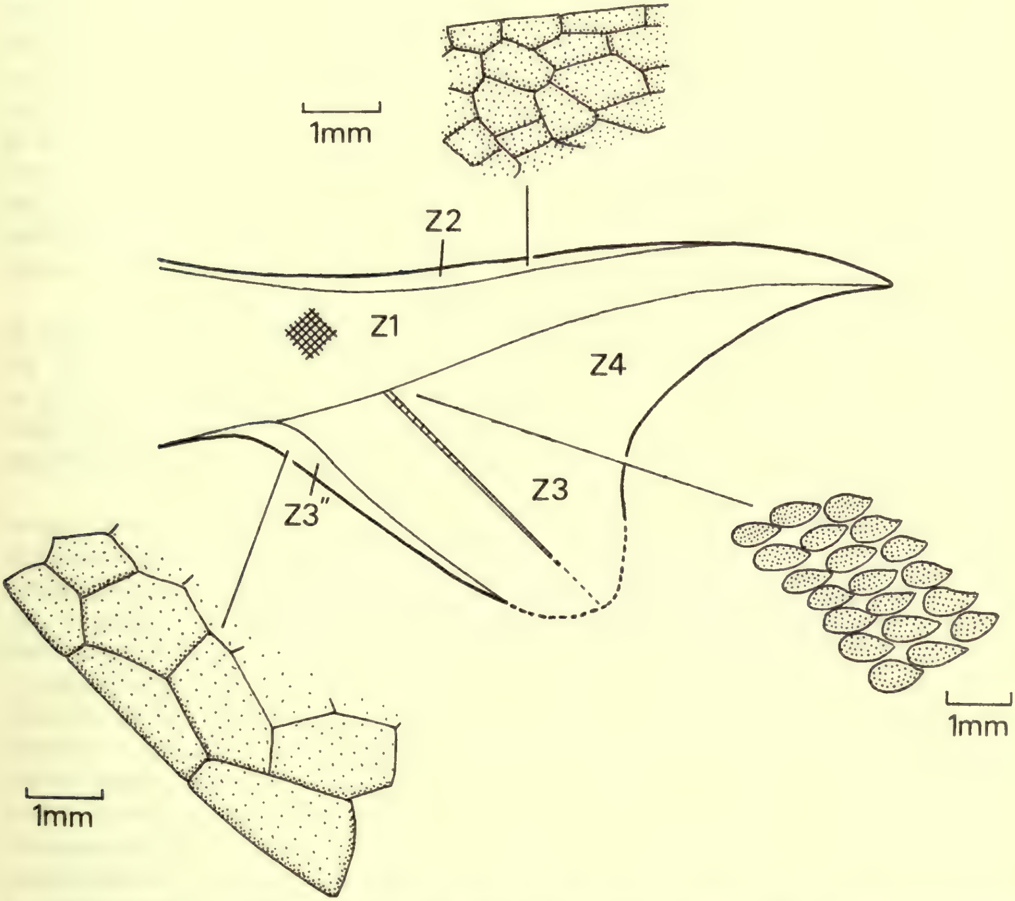
The scales on the webs of the dorsal and anal fins are fundamentally the same as the flank scales. The central navicular area is, however, long and narrow, and there are no lateral areas or lateral points (Text-fig. 1D). As in other acanthodians, the fin scales are arranged in long, straight rows.



Text-fig. 2. *Ptomacanthus anglicus* gen. et sp. nov. Lower Old Red Sandstone. Flank scales bordering the main lateral-line. BM P.16615. Ditton series, Wayne Herbert quarry, Newton, Herefordshire, England.

The squamation of the tail can be compared with that of *Acanthodes*, in which four scale zones have been described (Heyler 1969, Miles 1970). Zone 1 (*Z1*, Text-fig. 3) comprises normal body scales, situated on the caudal prolongation; they require no comment. Zone 2 (*Z2*) lies in an epichordal position, and in *Acanthodes* it comprised regular rows of scales set almost at right angles to the caudal prolongation, but with a differentiated outer region of smaller scales more posteriorly orientated (zone 2″). The scales of zone 2 are, however, not differentiated in this way in *P. anglicus*. Instead they form a mosaic of unornamented, thick scales, in which the basic regular arrangement has been lost. There is no sign of an axial caudal lobe, but a hypochordal lobe with distinct ventral and longitudinal divisions can plainly be seen. The scales of these divisions have been described as zones 3 and 4 (*Z3*, *Z4*) in *Acanthodes*, but there are no important differences between the scales of these divisions in *P. anglicus*. The scales are arranged in long rows, and become progressively finer distally. They have slightly depressed navicular crowns without ornamentation, which are arranged at right angles to the long axes of the rows. The most distal regions of the hypochordal lobe, with very fine scales, cannot be observed clearly, but it is likely that there is some branching of the scale rows here as in other acanthodians (Miles 1970 : 355). Anteriorly at the root of the ventral division of the hypochordal lobe, the scales are enlarged and somewhat irregularly arranged, as in zone 2. I propose to distinguish this region as zone 3″. An exactly comparable zone has been described in *Parexus falcatus* Powrie by Dean (1907 : 215, Text-fig. 20), and I have recorded a similar condition in *Ischnacanthus gracilis* (Egerton) and *Mesacanthus mitchelli* (Egerton) (Miles 1970 : 356) and briefly noted its functional significance.

If one excludes the tesserae of the head (*v. infra*) and the fin scales, there is remarkably little regional differentiation of the squamation in *P. anglicus*. The only notable variation from the standard type of (flank) scale occurs in the shoulder region, with flat lateral and blade-like ventral scales. This is in marked contrast to conditions in some sharks, e.g. *Heterodontus francisci* (Girard) (Daniel 1914), in which there are distinct dorsal and ventral scales with variously modified types of each. One type of dorsal scale occurs at the base of the pelvic fin and posterior to



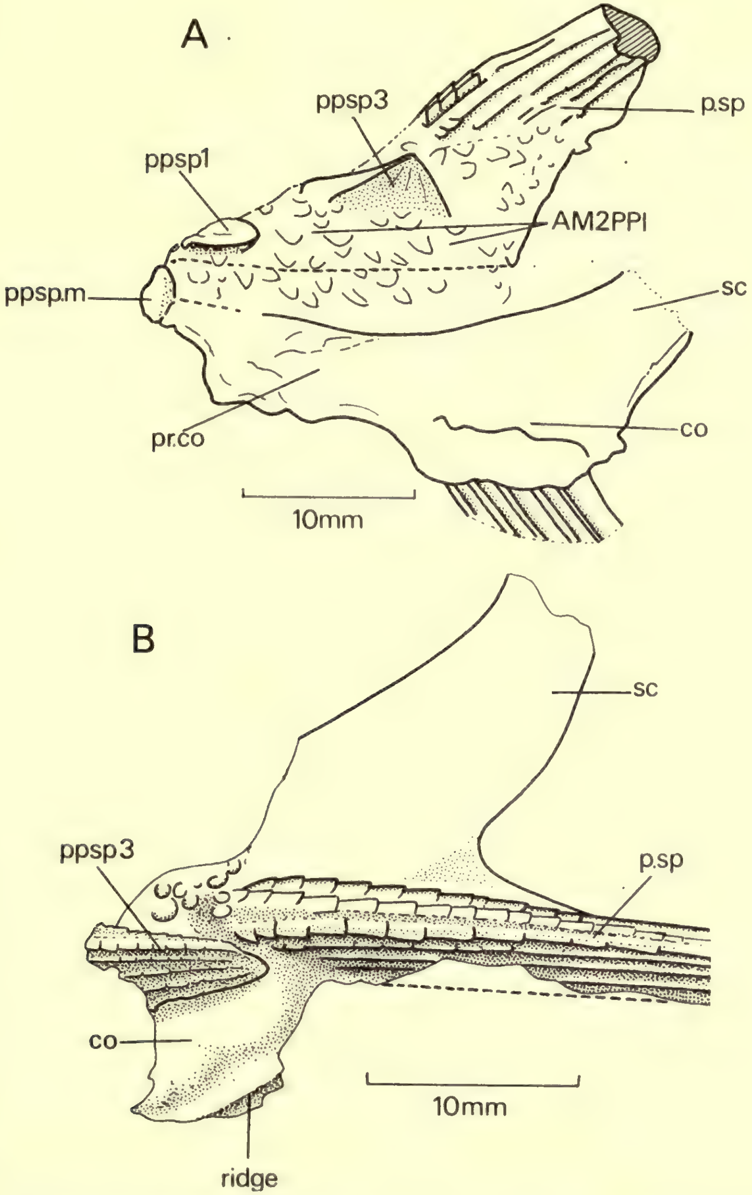
Text-fig. 3. *Ptomacanthus anglicus* gen. et sp. nov. Lower Old Red Sandstone. Regional differentiation of squamation on caudal fin. After holotype, BM P.19998–9 and BM P.53037. Ditton Series, Wayne Herbert quarry, Newton, Herefordshire, England.

the cloaca ('anchor scales'). Although the venter is well seen in one specimen of *P. anglicus* (BM P.20003), there is no indication of modified scales which might have been situated near the vent.

(iii) *Spines.* These are seen in the illustrations and may be described briefly. The prepectoral spines are noted below with the shoulder-girdle. The pectoral spine is not completely preserved, but is known to be moderately curved and ornamented on both its dorsal and ventral surface with six or seven ribs. These ribs bear nodes which are especially prominent proximally; they are of the familiar cone-like climatioid type with each node appearing to fit into the adjacent proximal node. The pelvic spine is also gently arched, and is ornamented with three ribs on both its dorsal and ventral surface. The anterior dorsal fin-spine resembles the pectoral in its size and curvature. It differs, however, in lacking nodes on the surface ribbing, except on the anterior margin. There are three or four ribs at either side. The posterior dorsal fin-spine is slightly shorter than the anterior and is almost straight, so that the two spines are distinct. Like the anterior spine, it is ornamented with three or four smooth ribs at each side, but in both cases imperfect preservation makes it difficult to be sure of the number. The anal fin-spine is slightly curved and bears five smooth ribs at each side. The intermediate spines are poorly seen in the holotype (Pl. 1, fig. 2) and in BM P.20003. There is no firm evidence of more than three (*v. infra*), of which the most anterior is situated some distance behind the shoulder-girdle. The first is the shortest and the last the longest, as is usual in climatioids, and all are ornamented with slender ribs.

(iv) *Shoulder-girdle.* In BM P.20003 the left side of the shoulder-girdle is seen in ventral view, and the right scapulocoracoid is seen in mesial aspect. Text-fig. 4A is a sketch of this specimen which may be used as a key diagram for Pl. 4, fig. 2. Text-fig. 4B is a drawing of a cast made from BM P.53285a, b, used as a two-piece mould; it shows much of the left shoulder-girdle in lateral aspect. Our knowledge is derived from these two specimens.

The scapulocoracoid has a broad scapular blade (*sc*) and deep coracoid region (*co*). The full height of the blade is not preserved, but it was presumably considerable. There is a long coracoid process (*pr.co*). More details of the scapulocoracoid may be obtained from other specimens of *Ptomacanthus* (p. 175), making it unnecessary to extend this account of *P. anglicus*. In front of the pectoral spine there are two lateral prepectoral spines (*ppsp 1*, *ppsp 3*; see p. 162*f* for terminology). The area mesial to these spines, under the coracoid process, is covered by the high crowned scales described above. Although the true conditions cannot be clearly seen in P.20003, evidence from *Climatius reticulatus* suggests that the pectoral spine, prepectoral spines and scales are attached to one or more thin, lateral dermal plates with ventral and ascending laminae, which are attached to the surface of the scapulocoracoid at a deep level in the corium (see pinnal plates, p. 163). Whether there were two median dermal plates as in *Climatius* is not clear, but there is evidently a median prepectoral spine (*ppsp.m*) which may have been attached to a small anterior plate (cf. anterior lorical, p. 163). The coracoid of P.53285 bears a low ridge (*ridge*, Text-fig. 4B) in the position of the first intermediate spine of *Climatius* and other


A
ppsp3
p.sp
ppsp1
AM2PPl
ppsp.m
sc
pr.co
co
10mm
B
sc
ppsp3
p.sp
co
10mm
ridge

TEXT-FIG. 4. *Ptomacanthus anglicus* gen. et sp. nov. Lower Old Red Sandstone. A, shoulder-girdle; key-diagram for Pl. 4, fig. 2. BM P.20003. B, shoulder-girdle in lateral view, from a cast. BM P.53285a, b. Ditton series, Wayne Herbert quarry, Newton, Herefordshire, England.

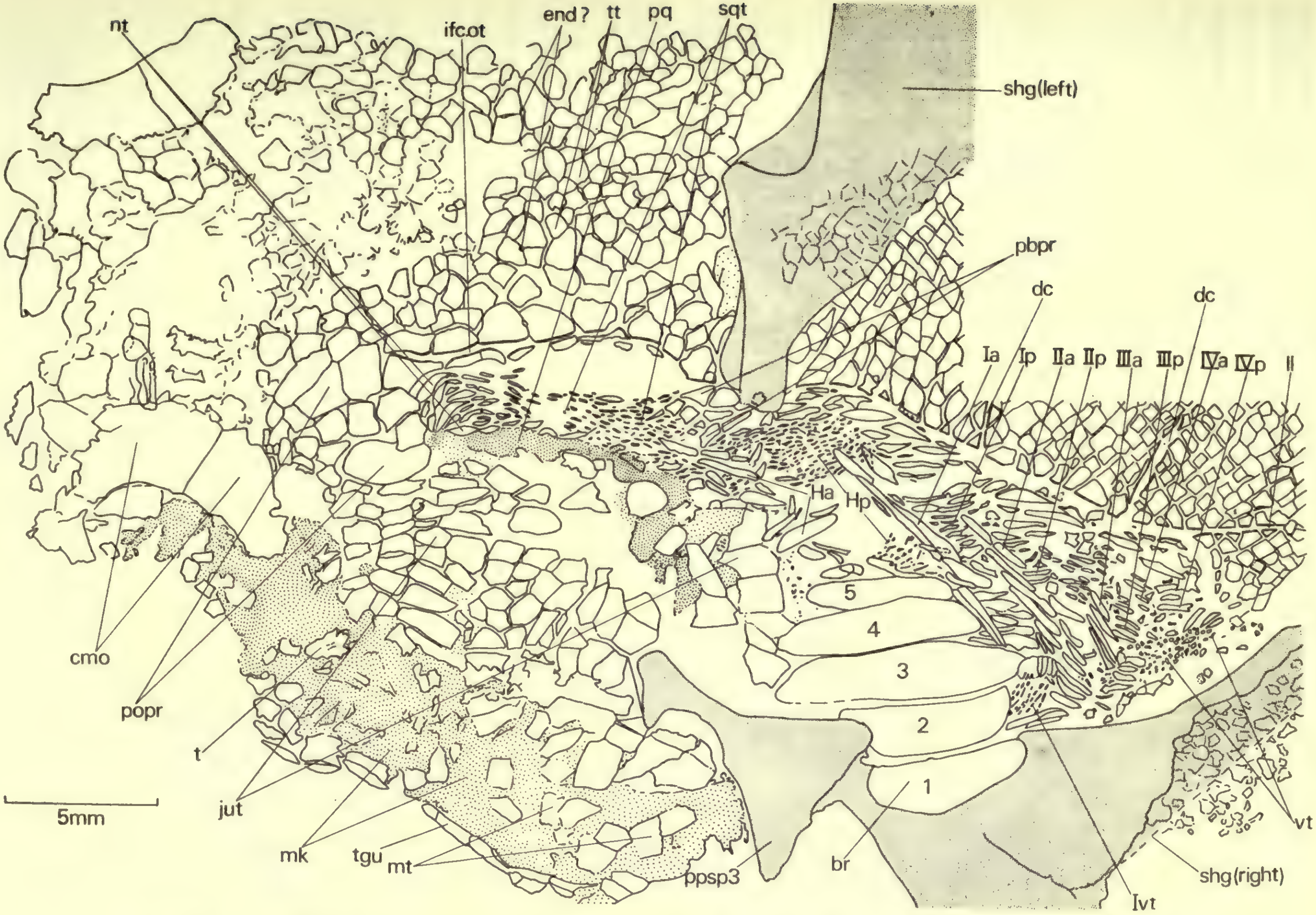
genera (p. 165), which is attached to the shoulder-girdle. P.20003, however, provides no supporting evidence of a ventrally directed spine in this position, and I provisionally conclude that it was absent. Further material may modify this view.

(v) *Gut contents.* The holotype (BM P.19998–9) had a head-shield of *Cephalaspis* sp. within the little-disturbed squamation of the posterior region of the visceral cavity. The animal appears to have been swallowed whole, head first, in the way that prey are ingested by many modern fishes. Denison (1956 : 426) records: 'That this *Cephalaspis* had actually been eaten is supported by the fact that it is the only small individual and the only non-articulated specimen of this genus in the lenticle, and also by the poor preservation of its surface, which suggests that it had been acted on by digestive juices.' The bone tissue of the specimen has been completely removed during preparation, but the *Cephalaspis* is clearly seen as an impression and in casts (Pl. 1, fig. 2). The tail of the *Cephalaspis* appears to have been disarticulated, but the squamation of the acanthodian is destroyed in this region.

(vi) *Head of Climatius reticulatus.* Although the head of *P. anglicus* shows some details of structure more clearly than any previously described climatiid, notably of the dentition and lower jaw, the whole structure can be described most satisfactorily by comparison with *C. reticulatus.*

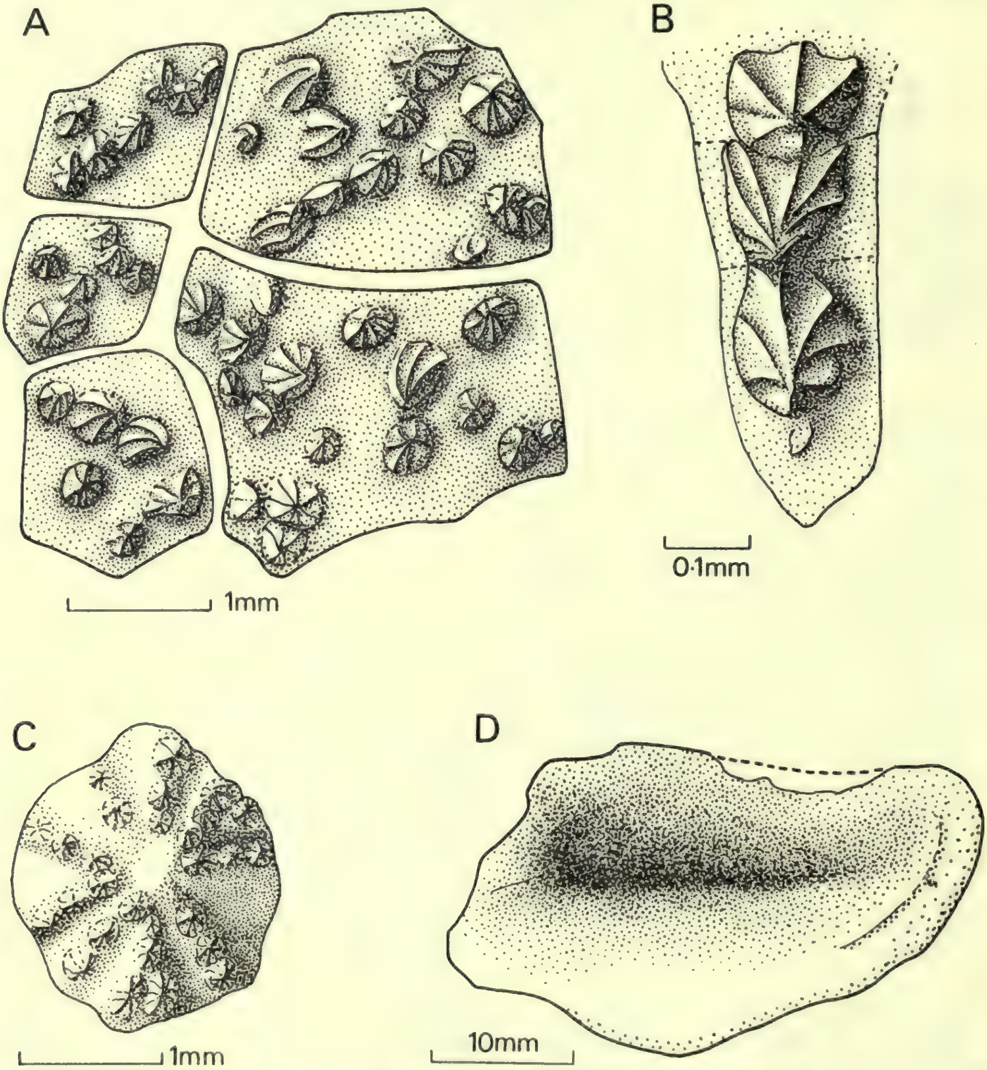
Shortly after I commenced the study of acanthodians in Stockholm in 1964, it became apparent that Watson's (1937) account of the dermal head skeleton in *C. reticulatus* does not always correspond with the structures shown by the specimens in his photographs. This is important because Watson's interpretations of other acanthodians are founded on *C. reticulatus*, and his restorations are used as evidence for his Aphetohyoid hypothesis. However, at that time the specimens available did not permit me to come to a satisfactory new interpretation, and the specimen I figured has since proved in some respects to be seriously misleading (Miles 1966 : 169, Text-fig. 9). Subsequently I continued to study *Climatius* in the Royal Scottish Museum (1964–1968), and I have now completed this work in the British Museum (Nat. Hist.). Shortly after the publication of Watson's (1937) paper, Dr C. Tate Regan restudied specimens in the British Museum (Nat. Hist.) with a view to contesting Watson's interpretation of the exoskeleton of the branchial region. Unfortunately Regan died before this work was finished, and although Dr E. I. White attempted to edit his notes for publication, this proved impossible. Later Holmgren (1942) published on the acanthodian head, and reached similar broad conclusions to Regan. I have carefully read Regan's manuscript, and although our interpretations do not always agree, I am indebted to him for a number of stimulating observations.

An account of the head of *Climatius reticulatus* must be based on BM P.1343 (misquoted throughout by Watson as 38596) and its counterpart RSM 1891.92.198, from the Lower Old Red Sandstone of Turin Hill, Angus, Scotland. This fish reveals the skeleton of the head in an unusually complete state. It is crushed flat and has been split open so that P.1343 shows the exoskeleton of the skull-roof, right cheek, lower jaw and branchial region, all in visceral view (Text-fig. 5; Pl. 2); whilst RSM 1891.92.198 (Watson 1937, Pl. 5, fig. 1) shows an impression of the right branchial


nt
ifcot
end?
tt
pq
sqt
shg(left)
pbpr
dc
dc
Ia
Ip
IIa
IIp
IIIa
IIIp
IVa
IVp
ll
Ha
Hp
5
4
3
2
1
cmo
popr
t
jut
mk
tgu
mt
ppsp3
br
lvt
shg(right)
vt
5mm

TEXT-FIG. 5. *Climatius reticulatus* Agassiz. Lower Old Red Sandstone. Plan of head; key-diagram for Pl. 2. BM P.1343. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

region and part of the skull-roof, the right gular tesserae in visceral view and part of the meckelian cartilage. The roofing (tectal, *tt*) tesserae are somewhat disturbed anteriorly and confused with the mandibular teeth (*t*), posteriorly the left and right shoulder-girdle bones (*shg*) have been displaced forwards into the branchial region, and the cheek has been pulled away slightly from the roof. Nevertheless the cheek



TEXT-FIG. 6. *Climatius reticulatus* Agassiz. Lower Old Red Sandstone. A, tectal tesserae, after RSM 1887.35.5A. B, ornamentation of circumorbital plate, after RSM 1887.35.5B. C, tessera from interorbital position, after BM.38596. D, visceral surface of lowest tessera of postorbital projection, after BM P.1343. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

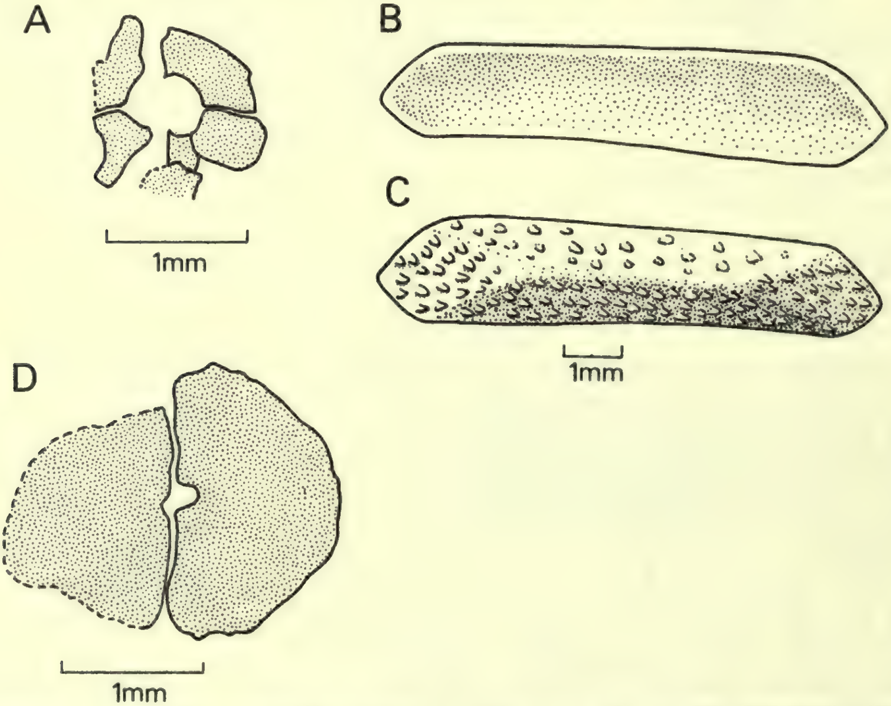
and branchial regions are little disturbed, and appear to show their true relationships and structure. The ornamentation of the tesserae and the structure of the jaw cartilages must be taken from other specimens. Watson (1937 : 52) has accurately described the granular appearance of the jaw cartilages; they have neither the character of perichondral bone nor of chondrichthyan calcified cartilage, and are of uncertain composition. Ørvig's (1951 : 412–415) study of other genera, however, suggests that they may be subperichondral calcified cartilage.

The orbit is surrounded by six transversely arched, stout plates (*cmo*, Text-fig. 5), which comprise two broad dorsals, two narrow ventrals, a small anterior and a posterior. They are ornamented with high, ridged denticle-like tubercles, which tend to fuse in rows across the surface (Miles 1966, Text-fig. 9; Pl. 10, fig. 1). In some specimens the circumorbital plates appear to be composed of fused tesserae, each with one tubercle (Text-fig. 6B; cf. Gross 1971, Pl. 2, figs. 10, 18). Immediately behind the posterior dorsal circumorbital plate a group of large tesserae marks the position of the underlying postorbital process of the neurocranium (*popr*, Text-fig. 5). The large ventral tessera of this group (the postorbital projection of the tectal field) has a deeply concave visceral surface (Text-fig. 6D).

Behind the postorbital group, the tesserae change character markedly at the infraorbital (otic branch) – main lateral-line (*ifc.ot*, *ll*). The lateral-line may conveniently be used to delimit the lateral extent of the tectal tesserae, but the difference in size between the elements above and below the lateral-line led Watson (1937 : 53, 56, also Miles 1966, Text-fig. 9) into the serious error of regarding the upper tesserae as marking the edge of a gill-chamber which stretched from the postorbital projection to the scapular blade. The lower tesserae are not shown in his illustrations (Watson 1937, Text-fig. 1, overlay to Pl. 5, fig. 2) and are discounted as having 'perhaps turned downward to the inner surface of the gill chamber'. Some 15 mm behind the postorbital projection there is a second lateral extension of the tectal tesserae, the prebranchial projection (*pbpr*, Text-fig. 5). Unfortunately this area of the skull-roof is disturbed by the displaced left half of the shoulder-girdle.

The scales of the trunk give way to the tectal field abruptly, along an oblique line which extends from just above the prebranchial projection almost to the otic region in the middle line. The arrangement of the tectal tesserae has been described by Watson (1937 : 53–56). On the outer surface the tesserae bear an ornament of ridged tubercles, which on some plates are still more densely packed than shown in Text-fig. 6A. These plates resemble some of the tesserae coronatae of *Nostolepis striata* Pander, which Gross (1971, Pl. 3, fig. 13) suggests were situated dorsally on the head. More anteriorly, between the circumorbital rings, the character of the plates changes. They become thicker and the tubercles tend to fuse into stout, radiating ridges (Text-fig. 6C; Dean 1907, Text-fig. 15). These plates are similar to certain tesserae stellatae of *N. striata* (Gross 1971, Pl. 2, figs. 25–26), although in this species Gross suggests they come from the underside of the head. The stellate tesserae are particularly well developed along the upper margin of the mouth, under the orbits and across the snout (BM 38596, RSM 1887.35.5c). This belies Watson's remark that the mouth 'has no distinct borders'. Watson described a possible nasal opening in RSM 1891.92.206. A similar fenestra can be seen in BM P.1343a, surrounded by five tesserae (Text-fig. 7A). A striking feature of the snout, as preserved, is the small distance that the tesserae extend in front of the circumorbital rings. This is important in making restorations of the snout, as Watson realised, and with other factors it makes it difficult to accept much of Holmgren's (1942) discussion of the basicranium and snout in acanthodians, which is based on conditions in selachians.

Watson (1937 : 54) has produced evidence of an opening for the ductus endolymphaticus in BM P.1343 (*end*?, Text-fig. 5). 'There is only one recognisable irregularity in the roof of the skull in this region, the presence, a little to each side of the mid-line of a pair of rather larger bones which meet one another in a straight transverse suture. On the left side in this suture there is a very minute foramen whose border lies mainly in the posterior bone; the opening is less clearly seen on the right.' Paradoxically I cannot confirm Watson's (1937, overlay to Pl. 5, fig. 2) interpretation of the tesserae surrounding the foramen in BM P.1343, but I find tesserae of exactly this form in BM 38596 (Text-fig. 7D). I am, however, not convinced that the foramen is the opening of the endolymphatic duct, because the



Text-fig. 7. *Climatius reticulatus* Agassiz. Lower Old Red Sandstone. A, circumnasal plates, BM P.1343a. B, C, branchiostegal ray in visceral and superficial view, restored after BM.38596. D, tectal tesserae surrounding endolymphatic or sensory-line opening, BM.38596. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

lateral-lines of the roof open to the surface through exactly similar foramina, and corroborative evidence of the duct has not been found in other acanthodians. On the present evidence the foramen can equally well be interpreted as the opening of the duct or for the supratemporal sensory line. A more laterally situated foramen in BM P.1343 supports the second view (Text-fig. 5). I do not dissent from Watson's interpretation of the other sensory lines, except to add that the otic branch of the infraorbital line appears to continue forwards above the postorbital tesserae as the 'profundus' line (*pfc*, Text-fig. 10; Miles 1966, Text-fig. 9, interpreted as edge of gill chamber), and there is evidence of the cheek (supramaxillary) line in BM P.6961 (*sml*, Text-fig. 10).

Although they are slightly displaced, the tesserae along the lower margin of the infraorbital (otic branch) – main lateral-line can be followed almost without a break from the postorbital projection (*popr*) back over the gill region (Text-fig. 5). Ventral to these tesserae, between the postorbital and prebranchial (*pbpr*) projections of the tectal field, there is a field of smaller tesserae which has pulled slightly away from the lateral-line. These may be termed the squamosal tesserae (*sqt*). Watson (1937 : 56, Text-fig. 1) interpreted them as having a position in the dorsal region of the mandibular operculum, and in his restoration he depicted the whole field as markedly more extensive than it appears in the fossil. The tesserae seem to be arranged essentially in horizontal rows, except most anteriorly where they increase in size and are navicular (*nt*), and are said by Watson to be 'arranged in a sickle shape'. These anterior elements mark the transition from the small horizontally placed squamosal tesserae to those of the postorbital projection, and it is doubtful whether they have any deeper morphological significance.

Ventral to the postorbital projection of the tectal field and the squamosal field, lie the tesserae of the cheek (*jut*). These jugal tesserae are tesserae stellatae, and except for some slight elongation they are closely similar to those of the roof. Similar tesserae cover the lateral surface of the lower jaw (*mt*), and the two groups were continuous over the adductor mandibulae musculature. The cheek tesserae accurately mirror the shape of the palatoquadrate, with a series of well defined elements attached to the upper rim of this cartilage bone. BM P.6961 shows that Watson erred in stating that the anterior ends of the branchiostegal rays ('mandibular rays') were attached to the outer surface of the jaw bones; they follow immediately posterior to these bones.[1] For the most part the cheek tesserae seem to be arranged in irregular vertical rows, as can be seen in the anterior region of BM P.1343. Posteriorly they are not well seen, but probably the rows have a more diagonal arrangement, like the mandibular tesserae (Watson 1937, Text-fig. 1).

The most ventral mandibular tesserae form two or three rows of low, elongated elements (*mt*), which are transitional to the still smaller, more elongated gular tesserae (*tgu*) on the chin. These tesserae form a pair of lateral fields, and are arranged 'in festoons parallel to the lower jaw' (Watson 1937 : 56). It is clear, as in other acanthodians, that there are no free-standing gular membranes (Miles 1966 : 153).

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[1] Watson (1937 : 56) writes of 'a series of very large thick bony rays (*Mand. Ray*), whose long dorsal and ventral borders are in contact with one another'. And . . . 'these opercular rays are attached by their anterior ends to the outer surfaces of the articular ends of the palato-quadrate and Meckel's cartilage'. If both of these statements are true it is difficult to see how the fish could have effectively opened its mouth.

In BM P.1343 there are five large branchiostegal rays (*br*) which I have numbered from the most ventral upwards in Text-fig. 5. The whole series has been slightly displaced posteriorly by the shoulder-girdle, but the second ray appears to have been situated at the level of the mandibular joint. In visceral aspect the rays are slightly hollowed and trough-like. On the outer surface they bear a median ridge which is flattened at either end (Text-fig. 7B, C). The branchiostegal rays are ornamented with ridged tubercles, like the tesserae. Above the 5th ray there is a series of smaller elements (*Ha*), which are somewhat disturbed, but probably each element is steeply inclined and the whole series leads up to the prebranchial projection. It is difficult to decide whether the apparent topmost element belongs to this series or to the lower edge of the projection. Behind these smaller rays there is a series of fine tesserae (*Hp*), which is interrupted (post-mortem?) and thus divided into separate dorsal and ventral groups. Comparisons with the succeeding branchial arches (*v. infra*) suggest that the groups of elements labelled *Ha* and *Hp* are related respectively to anterior and posterior exoskeletal series in the dorsal region of the hyoid (i.e., the main) gill-cover, above the branchiostegal rays. Watson's interpretation of the structures in this region is different. He shows a larger, more uniform series of branchiostegal ('mandibular') rays, which extends up to the top of the jugal field of tesserae, where it is contiguous with the squamosal tesserae ('mandibular operculum'). Behind the branchiostegal rays he depicts an extensive group of small tesserae ('ossicles') which extends the ('mandibular') operculum back across the lower region of the branchial region almost to the shoulder-girdle. Ventrally these elements run down into the gular tesserae.

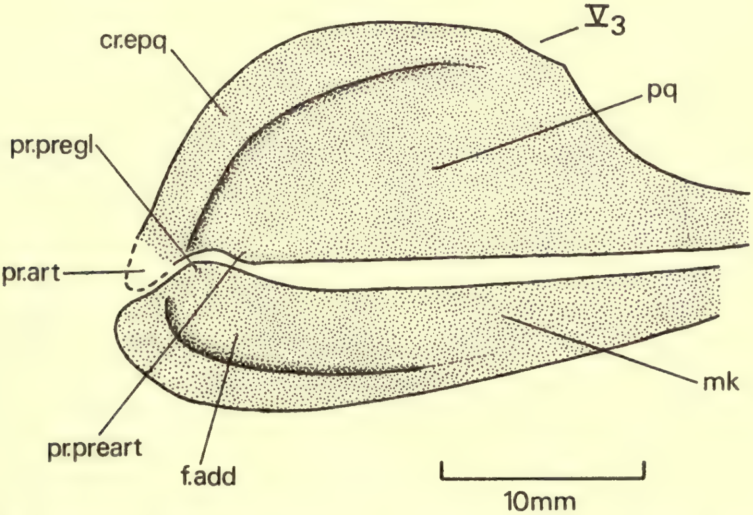
There is evidence of four branchial arches behind the hyoid gill-cover. They appear to be fundamentally the same as each other with respect to the exoskeleton, although their structure is progressively less well seen from the first one backwards. The scales are slightly displaced at the hind end of the branchial region, and it is not obvious that the gill-chamber had a definite posterior margin in the flank squamation. The exoskeleton of each gill-cover comprises an anterior series of elongated, obliquely placed elements (*Ia–IVa*), which are arranged in an irregular echelon; and a posterior series of smaller, more horizontally placed elements (*Ip–IVp*). The posterior elements are subject to some dorsoventral differentiation. Dorsally they increase in size, extend forwards to replace the anterior, oblique elements, and are transitional to the tesserae which form the lower margin of the main lateral-line. Ventrally they appear to dissolve into small scales (*vt*), which are presumably transitional to the scales overlying the scapulocoracoid, although this region cannot be clearly observed. The small ventral scales of the first gill-cover (*Ivt*) were probably included by Watson in the 'mandibular operculum'.

The arrangement of the exoskeleton of the gill-arches can be readily understood if it is assumed that the anterior series of elements were situated on the free ends of the gill-septa, and the posterior series on the outer surface of the gill-flaps.

The jaw cartilages of *Climatius* can be studied in BM P.6961 and GSM 49785 (Pl. 3), on which Text-fig. 8 is based. The details are not clearly seen, but it seems beyond question that Watson was correct in claiming the absence from the palatoquadrate of the otic process found in *Acanthodes*. A shallow notch in the dorsal margin (V_3) may mark the passage of the r. mandibularis trigemini and external carotid artery. The lateral face of the palatoquadrate bears an extrapalatoquadrate ridge (*cr.epq*). There is no sign anteriorly of a basal or orbital process, and no evidence that the palatoquadrate extended forwards in a palatine process to meet its antimere in the middle line (cf. *Acanthodes*, Miles 1968 : 120). The meckelian cartilage bears a lateral fossa for the insertion of the adductor muscles (*f.add*). There is no indication of a dermal mandibular bone. The mandibular joint is obscure, but it is possible that it was double as in *Acanthodes bronni* (Miles 1968), as there is some evidence of a prearticular process of the palatoquadrate (*pr.preart*) and a preglenoid process of the meckelian cartilage (*pr.pregl*).

Most specimens of *Climatius* have the dentition preserved (see e.g. Pl. 3), but the teeth are always so disturbed that it is impossible to obtain a complete picture of their form and arrangement. They seem, however, to be restricted to the lower jaw, and are shown somewhat diagrammatically in Watson's (1937, Text-fig. 1) reconstruction of the head. The dentition is seen more completely in *Ptomacanthus anglicus* and the following notes are given mainly to supplement Watson's account and provide a basis for comparison.

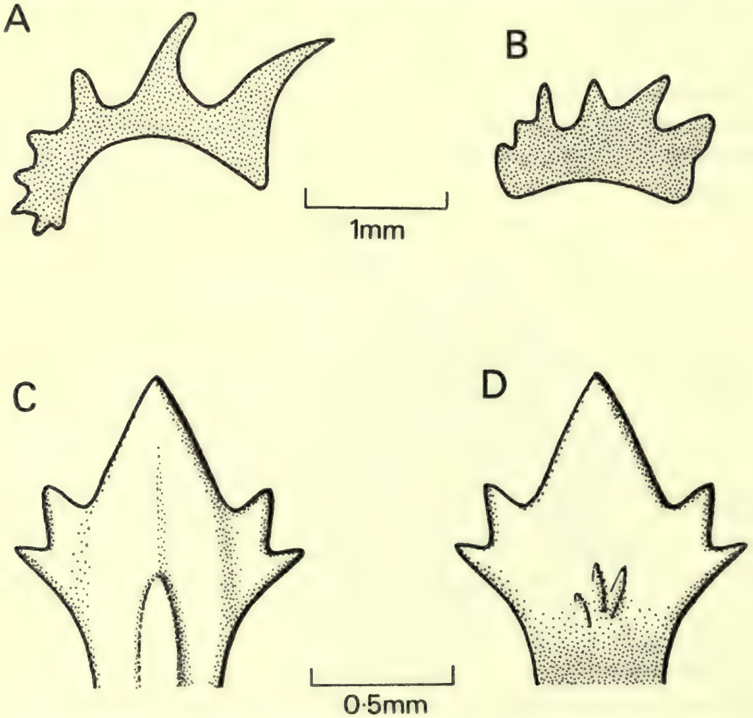
Each tooth has an arched basal plate placed transversely across the margin of the jaw, and a number (maximum at least seven) of cusps (Text-fig. 9; Miles 1966, Pl. 10).



TEXT-FIG. 8. *Climatius reticulatus* Agassiz. Lower Old Red Sandstone. Right palatoquadrate and meckelian cartilage in lateral view. After BM P.6961 and GSM 49785. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

The teeth have usually been split through their substance in the rock, and there appears to be much variation in the thickness of the basal plate and in the length and number of the cusps. The true variation in these respects cannot be estimated. The principal cusps seem clearly to increase in height in the lingual direction, and most labially they have almost the character of the dermal ornamentation. Comparable conditions are found in *Nostolepis* (Gross 1957, 1971). In labial and lingual view the principal tooth cusps are seen to be broad and thin, and to have two pairs of smaller side cusps, which are almost symmetrically placed. Towards the base of each principal cusp the surface is thickened by a broad ridge in some cases, and bears several slender ridges in others. It is tentatively suggested that the first condition is seen on the labial face of the cusp (Text-fig. 9C), and the second on the lingual face (Text-fig. 9D). The broad ridge has been incorrectly labelled as a tooth cusp in an earlier work (Miles 1966, Pl. 10B).

Because of the curvature of the basal plate, it is customary to term the climatiid tooth a tooth-whorl or spiral (see also ischnacanthids), but these names are misleading if they imply the existence of a compound structure. Thus Watson (1937 : 53) writes that the dentition is 'composed of fused whorls of teeth', and the 'whorl



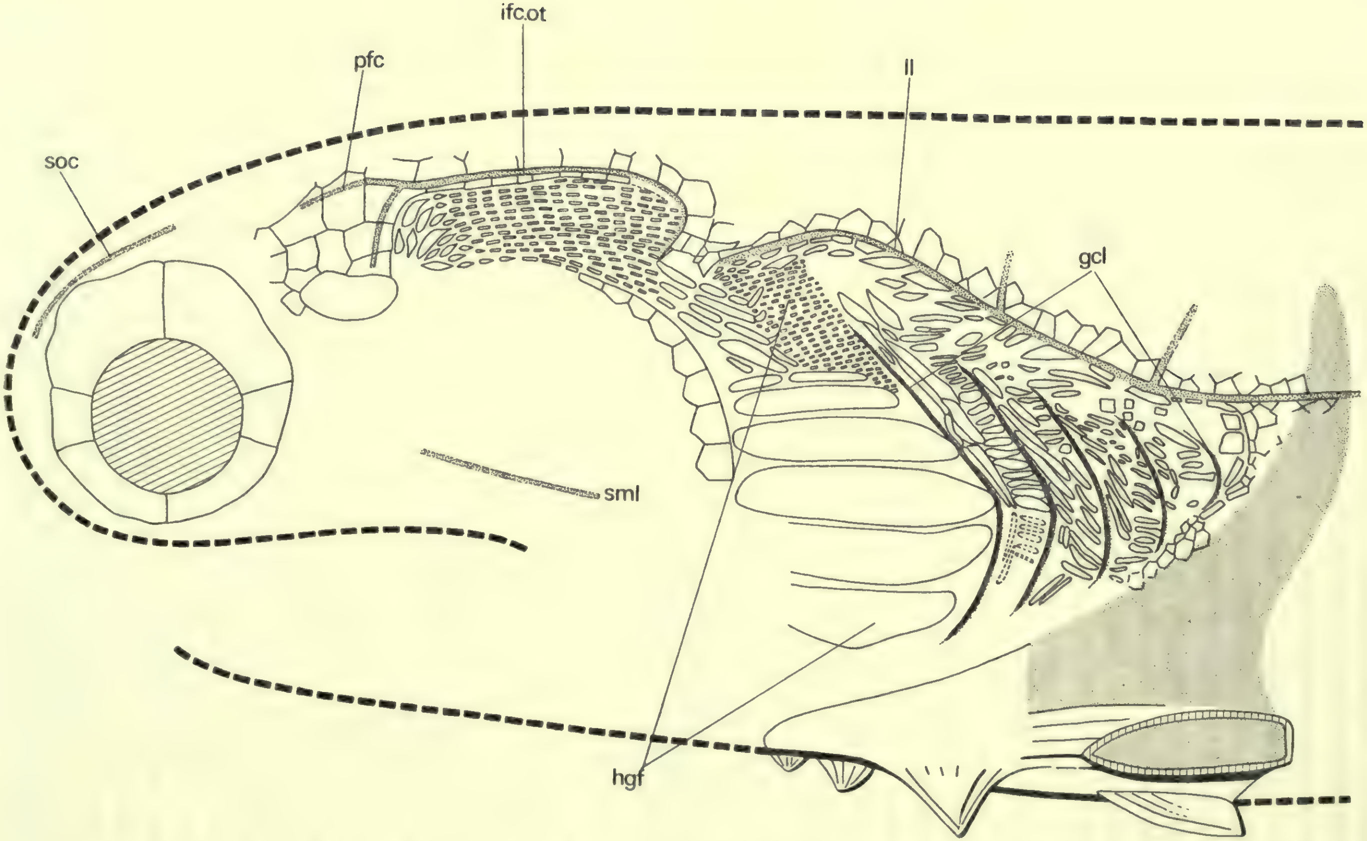
TEXT-FIG. 9. *Climatius reticulatus* Agassiz. Lower Old Red Sandstone. Jaw teeth. A, section after GSM 49785; B, section after BM 38596; C, D, labial and lingual surfaces of cusp respectively after RSM 1887.35.5C and BM P.1343. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

seems to consist of at least three teeth'. I have propagated this error by suggesting that in climatiiforms the teeth apparently 'underwent a regular replacement which simulated the elasmobranch method' (Miles 1965 : 245, also 1971 : 68). However, Gross (1957 : 7) has suggested that all the cusps ('teeth') of the tooth ('spiral') were formed at the same time; that the growth of the tooth did not involve the addition of new cusps; and there is no evidence of tooth replacement. The absence of replacement in climatiids is confirmed by the specimens of *P. anglicus* described below. The teeth are thus not closely comparable with those of elasmobranchs. Whether these remarks also apply to the tightly inrolled teeth of primitive ischnacanthids (*Gomphodus*) is not clear (Woodward 1891, Pl. 15, fig. 1; Gross 1957, Pl. 2, figs. 1, 2, Pl. 3, figs. 1, 4), but Gross (1971 : 28) has recently suggested that even teeth of the *Nostolepis* type could grow by the addition of new cusps.

The dentigerous jaw bones of *Nostolepis* and ischnacanthids (Gross 1957, 1971; Ørvig 1967) can be regarded as equal to a series of *Climatius* teeth which have fused together and undergone marked differentiation of the cusps. Ørvig (1967 : 147) stresses that each principal cusp and its side cusps in these jaw bones represents a single tooth, and not a family of teeth ('Zahnfamilien') as originally supposed by Gross (1957 : 12, but see 1971 : 26). Thus, there are no true *marginal tooth-bearing bones* in acanthodians (Miles 1965 : 244), as this expression is normally understood (e.g., Westoll 1949 : 159).

I do not think it is possible to draw an accurate restoration of the head of *Climatius* with the materials now available. Text-fig. 10, therefore, claims to be no more than a diagrammatic attempt to represent the gill region, in which the mutual relations of the main bones are correct in principle. It is based on BM P.1343, and no allowance has been made for the curvature of the cheek and gill region that must have been present in life. Five separate gill-clefts (*gcl*) are shown decreasing in size in the posterior direction. They resemble the gill-clefts of elasmobranchs, but this condition of the branchial openings has long been thought to be primitive for gnathostomes (e.g. Goodrich 1909 : 95). On the other hand, the enlarged first gill-flap (*hgf*) with large branchiostegal rays foreshadows the osteichthyan condition. The enlarged first gill-flap has the same morphological relationships as the hyoidean gill-cover of other fishes, and I reject Watson's conclusion that it belongs to the mandibular arch. The small tesserae in the dorsal part of the hyoid gill cover are not repeated in the more posterior arches. They may indicate the presence of a dorsal fold of flexible skin in this region, shaped somewhat like the fold in the hyoidean gill-flap of *Chlamydoselachus* (Allis 1923, Pl. 1; Smith 1937). In the post-hyoidean gill-arches the tesserae in the skin above the gill-clefts are loosely arranged, and show no definite pattern. Probably this indicates a flexible area, with the tesserae lying superficial to the dorsal constrictor muscles. By an extension of this argument, the squamosal field of tesserae may be related to that part of the dorsal constrictor musculature of the mandibular arch which passed from the palatoquadrate to the brain-case (m. levator palatoquadrati; cf. *Acanthodes*, Miles 1968 : 117).

Perhaps the most telling criticism of Watson's restoration is that it is not functionally convincing. Thus by Watson's own declaration the palatoquadrate has no


ifc.ot
pfc
ll
soc
gcl
sml
hgf

TEXT-FIG. 10. *Climatius reticulatus* Agassiz. Lower Old Red Sandstone. Sketch restoration of head in lateral view.

contact with the neurocranium[2], the hyoid arch is unmodified and non-suspensory, and the region above the palatoquadrate, which I believe was crossed by the mandibular levator muscles, is perforated by the anterior part of a very long, open spiracular gill-slit. If these conditions obtained, it is difficult to see how the upper jaw was held firmly in place in the head, or how it could have carried a large, mobile gill-cover.

The new restoration (Text-fig. 10) removes the evidence for a complete spiracular gill-slit and unmodified hyoid arch. There is no direct evidence bearing on the condition of this last structure, but the nature of the palatoquadrate suggests the presence of a suspensory hyomandibula, as in *Acanthodes*, and I believe that the jaw suspension was hyostylic.

(vii) *Head of Ptomacanthus anglicus.* The exoskeleton is well shown by P.24919 (Pls. 5, 6), and a number of points are confirmed by P.19998–9 and P.20002–3. There is, however, no sign of the lateral-line system. There is a stout circumorbital ring (*cmo*, Pl. 1, fig. 2, Pl. 5) with an undetermined number of plates, although there is evidence of two broad dorsal plates as in *Climatius*. Dorsally the trunk scales extend forwards over the branchial skeleton into the otic region. Here, as in *Climatius*, they are replaced by thick tectal tesserae (*tt*, Pl. 5). On the anterior surface of the snout the tesserae are enlarged into tesserae stellatae, whilst on the ventral margin they form a distinct row of smaller elements which interlock with the anterior teeth of the upper jaw (Pl. 6). A paired break in the tesserae of the snout is probably the exoskeletal nasal opening (*na*). There is no sign of the postorbital or prebranchial projection of the tectal field.

The tectal tesserae are not as distinctly separated from the jugal (*jut*) and squamosal (*sqt*) tesserae as in *Climatius* (Pl. 5). The different fields grade into each other over short distances. The jugal tesserae are tesserae stellatae. They are slightly larger than the tectal tesserae, and ventrally they merge with the large mandibular tesserae over the surface of the lower jaw (*mt*, Pl. 5). The last elements are arranged in rows much as shown by Watson for *Climatius*. The field of small jugal tesserae is, however, more extensive ventrally than in *Climatius*. Behind the lower jaw there are five slender branchiostegal rays (*br*, Pls. 5, 6), with an ornament of short, interlocking ridges on the outer surface. The more dorsal region of the hyoid gill-cover is unknown. Ventrally the mandibular tesserae give way to elongated gular tesserae (*tgu*, Pl. 6) closely similar to those of *Climatius*, but the lower surface of the head is not well preserved. It is possible that there are four gill arches behind the hyoid gill-cover, although the exact number cannot be given. The exoskeleton of each comprises an anterior series of upright elements (*br.a*) and a posterior series of horizontal elements (*br.p*, Pl. 6). These elements are stouter, and apparently more closely and regularly arranged than their homologues in *Climatius*, although this may simply be a matter of superior preservation in *P.*

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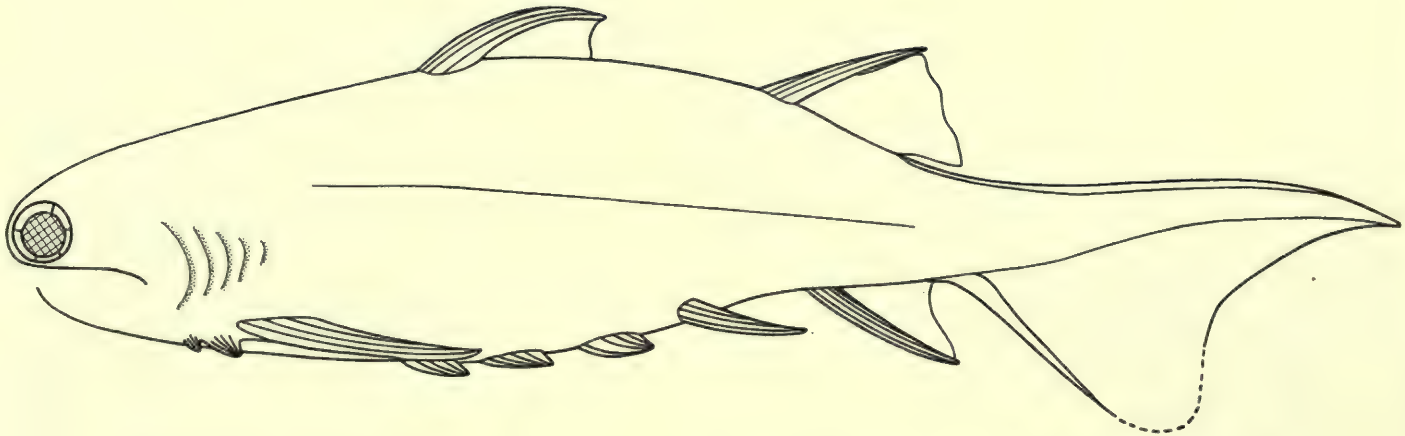
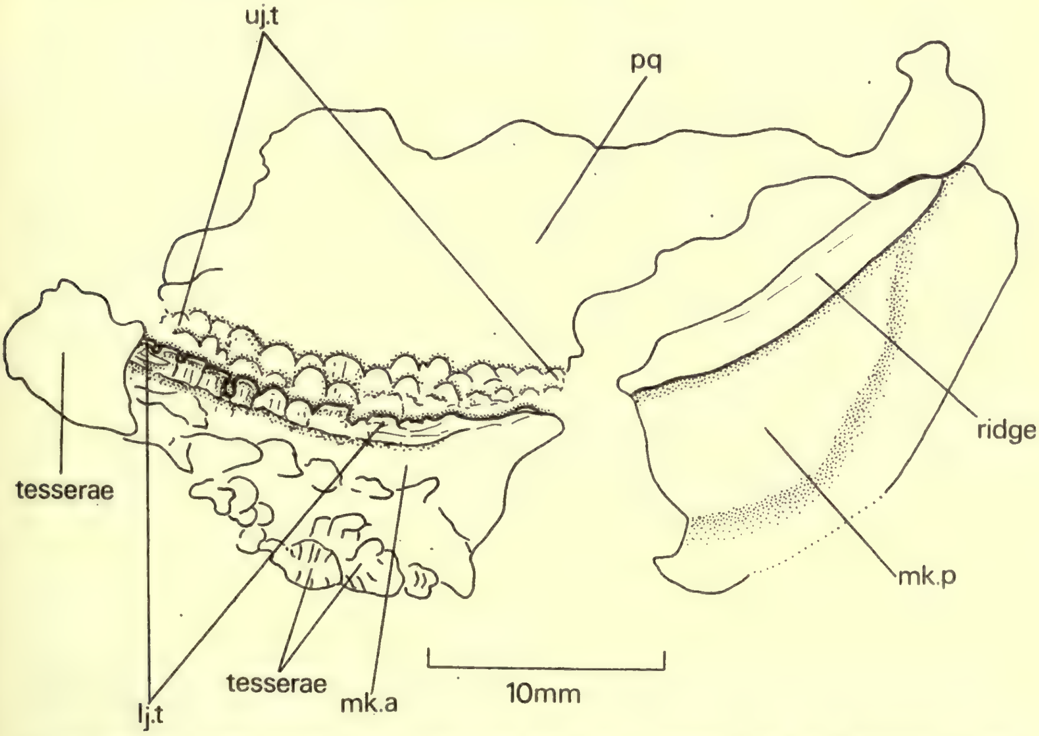
[2] I think there may have been a basal articulation, as in *Acanthodes*, even though there is no evidence of a basal process in the incomplete fossils.



TEXT-FIG. 11. *Ptomacanthus anglicus* gen. et sp. nov. Lower Old Red Sandstone. Restoration in lateral view.

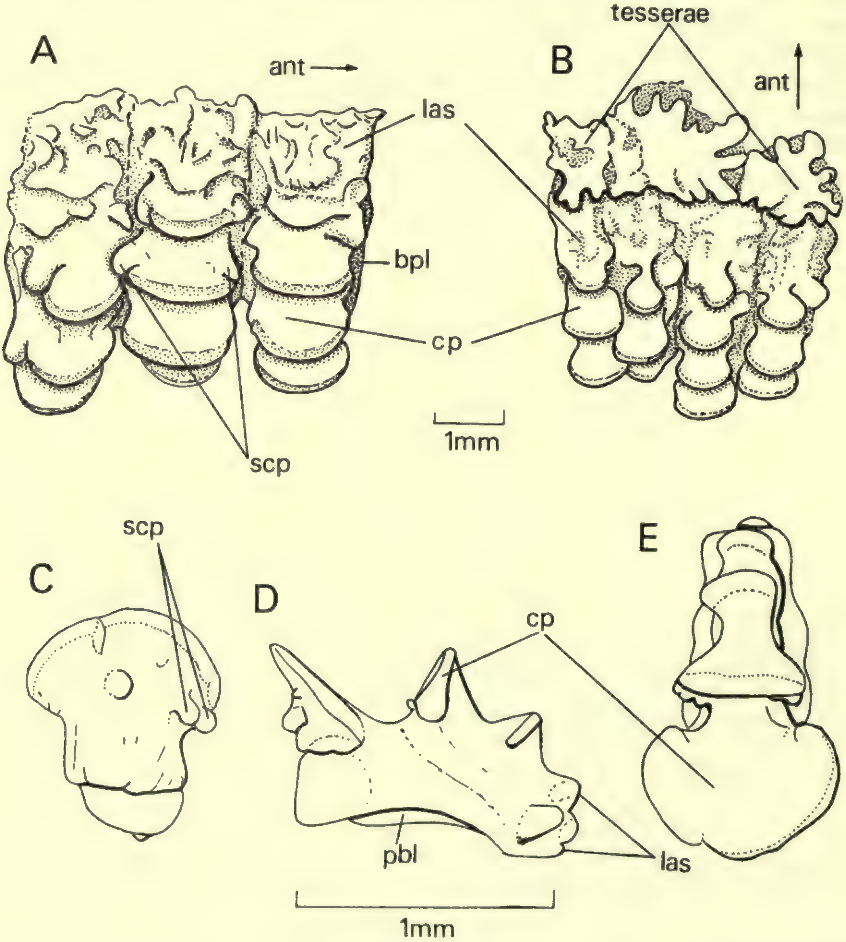
anglicus. There is no evidence of clear-cut margins to the gill-chamber in the exoskeleton, and this supports the new interpretation of *Climatius* given above.

In P.19998 the jugal and mandibular tesserae are pressed down over the outer surfaces of the right palatoquadrate and meckelian cartilage. The relief clearly shows the presence of a stout extrapalatoquadrate ridge and an adductor muscle fossa, as in *Climatius.* The palatoquadrate is also seen in other specimens (*pq*, Text-fig. 12, Pl. 1, fig. 2, Pl. 6), which confirm the lack of a palatine process and indicate a close similarity to *Climatius,* but add no details of structure. P.19999 (Pl. 4, fig. 1, use Text-fig. 12 as key-drawing) shows both the palatoquadrate and meckelian cartilage and demonstrates that there are teeth in both the upper and lower jaws (cf. *Climatius,* p. 131). The meckelian cartilage is calcified in separate anterior (*mk.a,* mentomandibular) and posterior (*mk.p,* articular) elements, as it is in a number of ischnacanthiform and acanthodiform genera (Watson 1937; Miles 1966, 1968), although this condition has not hitherto been recorded in a climatiiform. The lower jaw teeth extend along the full length of the anterior element; the dorsal margin of the posterior element is thickened into a ridge. There is no dermal mandibular bone on the lower margin of the jaw.



TEXT-FIG. 12. *Ptomacanthus anglicus* gen. et sp. nov. Lower Old Red Sandstone. Left lower jaw and palatoquadrate; key-diagram for Pl. 4, fig. 1. BM P.19999. Ditton Series, Wayne Herbert quarry, Newton, Herefordshire, England.

The teeth are best seen in P.24919a, which is illustrated by a photograph (Pl. 6). The upper teeth are preserved in an almost undisturbed arch, and comprise multicuspid structures which can be interpreted by comparison with the detached teeth of *Nostolepis striata*, which they closely resemble (Text-fig. 13; Gross 1957, Pl. 4, figs. 6, 7, 1971, Pl. 3, figs. 32–34). There is, however, no evidence in either the upper or lower jaws of the dentigerous jaw bones found in *N. striata* (Gross 1957, 1971; Ørvig 1967). The tooth row is continuous across the middle line and includes about 50 separate teeth packed closely together. The most anterior teeth measure



Text-fig. 13. A, B, *Ptomacanthus anglicus* gen. et sp. nov. Lower Old Red Sandstone. Groups of teeth in ventral view, from the lateral and rostral regions of the upper tooth arcade respectively, in B with adjacent tesserae. BM P.24919a. Ditton Series, Wayne Herbert quarry, Newton, Herefordshire, England. C, D, E, *Nostolepis striata* Pander. Upper Silurian. Tooth in lingual, anterior (or posterior) and dorsal view respectively. After Gross 1957, Pl. 4, fig. 7.

about 0·8 mm across the broad face of their largest cusps; from which the teeth increase in size posteriorly until this dimension is about 1·7 mm.

The individual teeth have an arched basal plate (*bpl*, Text-fig. 13A, B) with three or four blade-like cusps (*cp*); small polyp-like side cusps (*scp*) are also present on some teeth, as in *Nostolepis*. The labial surface of each tooth (*las*) is ornamented like the adjacent tesserae, and the teeth and tesserae are firmly interlocked with each other. This is conclusive evidence that the teeth were not elasmobranch-like, but were permanent growing units (p. 133), and it explains how the teeth were supported in a continuous row over the anterior margin of the upper jaw in the absence of a palatoquadrate symphysis (p. 137). Only the larger, more posterior teeth received additional support from the palatoquadrate, and it was these teeth that carried the main force of the bite. Unfortunately, the curvature of the basal plates is unknown, and the data provided by Gross (1957) cannot be related to the positions of the teeth in the jaws. It seems probable that the cusps of adjacent teeth were accurately aligned, so that they formed ridges following the margin of the jaw, but it is not possible to demonstrate this conclusively. It does seem clear, however, that all the cusps were functional and that the upper teeth accurately 'interdigitated' with those of the lower jaw.

DISCUSSION. The teeth, scales, tesserae and spines show that *Ptomacanthus* is a relatively primitive climatiid closely related to *Nostolepis* and *Climatius*. It differs from *Nostolepis* in the absence of dentigerous jaw bones, although the significance of this cannot be assessed, and resembles it strikingly in the form of the discrete marginal jaw teeth. This resemblance may indicate immediate consanguinity, as I believe, or may be due to parallel evolution. Further comparisons and conclusions can hardly be drawn in the absence of articulated specimens of *Nostolepis*. The above account has shown that *Ptomacanthus* and *Climatius* are fundamentally the same in the skeleton of the head. *Climatius* is, however, more advanced in the dentition, as it lacks upper jaw teeth, and more primitive in its heavily ossified shoulder-girdle (p. 163). *Erriwacanthus* (p. 166) is also more primitive than *Ptomacanthus* in the structure of the shoulder-girdle.

Of the more advanced climatiids, *Ptomacanthus* differs from *Brachyacanthus* in the absence of enlarged median dorsal scutes in front of the first dorsal fin-spine and in its longer fin-spines; and from *Parexus* in the absence of a greatly lengthened first dorsal fin-spine and in the structure of the shoulder-girdle (p. 181).

VERNICOMACANTHUS gen. nov.

DEFINITION. Climatiid fishes with an elongated body and moderately broad fin-spines; anterior dorsal fin-spine slightly curved and longer than pectoral fin-spine, but not as elongated as in *Parexus*; dermal shoulder-girdle reduced to anterior lorical, and ascending lamina of a compound pinnal plate, and with at least one paired prepectoral spine.

ETYMOLOGY. After the *Vernicomes*, the Caledonian tribe which inhabited that part of Southern Pictavia which is now in Angus, Scotland; and Gr. *akantha*, a thorn.

TYPE SPECIES. *Climatius uncinatus* Powrie.

REMARKS. *Vernicomacanthus* differs from *Climatius* in the structure of the shoulder-girdle (pp. 162–166; q.v. for terminology), and in the same way from *Erriwacanthus*, *Ptomacanthus* and *Brachyacanthus*. It is probably more closely related to *Parexus*, from which, however, it differs in the length of the first dorsal fin-spine. It also differs from *Brachyacanthus* in the absence of median scutes in front of the first dorsal fin-spine. *Vernicomacanthus* has up to six pairs of intermediate spines, i.e., the same number as some specimens of *Euthacanthus macnicoli* (Watson 1937 : 65) but more than any other articulated climatiid.

VERNICOMACANTHUS UNCINATUS (Powrie)

Pl. 7

1864 *Climatius uncinatus;* Powrie (ex Egerton MS), p. 422
1870 *Climatius uncinatus;* Powrie, p. 296, pl. 14, fig. 11
1891 *Climatius uncinatus;* Powrie, Woodward, p. 30

DEFINITION. A species attaining a length of 150 mm, with large curved pectoral spines bearing posterior denticles, and with six pairs of well-developed intermediate spines.

TYPE. The lectotype is RSM 1891.92.208 (Powrie 1870, Pl. 14, fig. 11).

MATERIAL. BM P.1342a, P.6960, P.1342; R S M 1891.92.209 and Kinnaird 82 (counterparts), 1891.92.210 and Mitchell 57 (counterparts).

LOCALITY. Turin Hill, Angus, Scotland.

HORIZON. Arbuthnott Group, Dundee Formation, Lower Old Red Sandstone.

REMARKS. The shoulder-girdle of this species is described below (pp. 176–180). The exoskeleton of the head is closely comparable with that of *Climatius reticulatus*, and several specimens (e.g. Pl. 7) confirm that Watson mistook lateral-lines of climatiids for the dorsal margin of the gill-chamber. The exoskeletal elements of the head are labelled in Pl. 7 to facilitate a direct comparison with the figures of *C. reticulatus* (Text-figs. 5, 10, Pl. 2).

VERNICOMACANTHUS WAYNENSIS sp. nov.

Pl. 1, figs. 1, 3, Pls. 8–10

ETYMOLOGY. After Wayne Herbert quarry.

DIAGNOSIS. A species differing from the type, *V. uncinatus*, in its greater size and in the lack of posterior denticles on the pectoral fin-spines, in the absence of a median prepectoral spine, in the reduction of the anterior lorical, and in the separation of this last plate from the ascending pinnal lamina.

TYPE. The holotype is an almost complete fish in part and counterpart, BM P.24938a, b (Pl. 1, figs. 1, 3, Pls. 8, 9, fig. 2).

HORIZON. Ditton Series, about 66 m above the main '*Psammosteus*' limestone, in the *Pteraspis crouchi* zone.

LOCALITY. Wayne Herbert quarry, near Newton, SW. Herefordshire; in the siltstone lenticle described by White (1935 : 383).

MATERIAL. This account is based on six individuals in the British Museum (Nat. Hist.); P.24938a, b, the holotype; P.16614, part of the flank in the region of the shoulder-girdle; P.16615, the ventral region of the flank with the dermal shoulder-girdle and the most anterior intermediate spines; P.52441a (Pl. 9, fig. 1), b (Pl. 10), most of the body forwards from the anal fin-spine to the branchiostegal rays, on the same slab as a specimen of *Pteraspis rostrata* figured by White (1935, Pe. 27, fig. 107); P.52443, the ventral region of the trunk with the intermediate spines.

DESCRIPTION. (i) *General features*. *V. waynensis* is a climatiid of moderate size, which reached a length of at least 140 mm. Incomplete preservation rules out a table of measurements of the fin-spines. The preservation of the specimens is comparable with that of *Ptomacanthus anglicus*, and it suggests a moderately slender body with a flattened venter and a broad skull-roof. It is difficult to obtain an accurate picture of the whole fish (Text-fig. 16), but it appears that the body is more elongated than in other genera of climatiids, and in this respect is comparable with *Euthacanthus* (Watson 1937, Text-fig. 4). In both *Vernicomacanthus* and *Euthacanthus* the length of the body and the large number of intermediate spines are probably correlated. There are six pairs in *V. waynensis* as in *V. uncinatus*. The pectoral and pelvic fin-spines are situated slightly in front of the transverse planes of the anterior and posterior dorsal fin-spines respectively (contrast *Euthacanthus*), and the anal fin-spine is inserted posterior to the level of the posterior dorsal (Pl. 1, fig. 1).

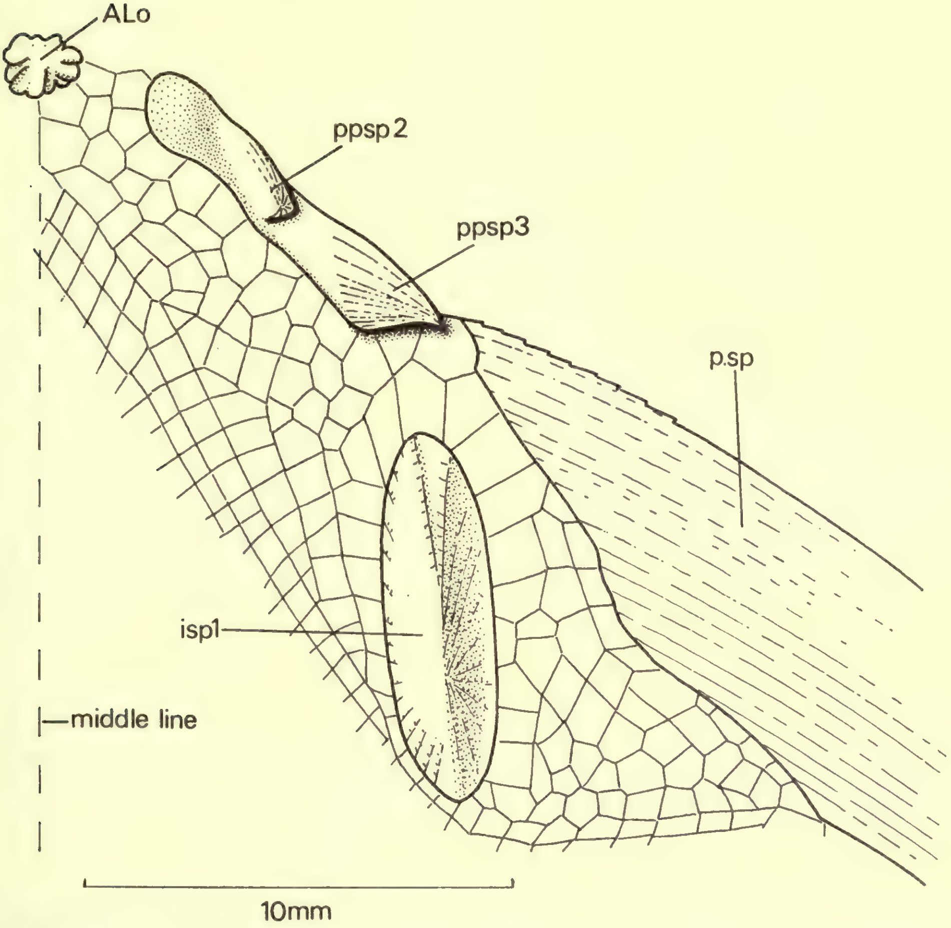
(ii) *Squamation*. The scales are typically acanthodian and encircle the body in oblique rows in the usual way (Pl. 1, fig. 1, Pls. 8, 10). The flank and ventral scales have the crown ornamented with a large central ridge, and one or two pairs of smaller side ridges, all of which are striated and end in free standing points (Pl. 1, fig. 3). The length of the crown is about 0·5 mm on the flank of the holotype. Towards the median dorsal line the scales increase in size, to almost twice their size on the flank (Pl. 1, fig. 1, Pl. 10), and the ridges become broken up into a network of connected tubercles. Enlarged scales are also found at the bases of the spines and on the lateral face of the scapulocoracoid (Pl. 1, fig. 1, Pls. 9, 10). The ventral surface of the body in the region of the pelvic and anal fin-spines is seen in P.52441a (Pl. 9, fig. 1). The vent cannot be satisfactorily delineated, but evidently it was not surrounded by special scales (p. 121). The left ventral lateral-line runs between rows of scales mesial to the intermediate spines in P.24938b (*vll*, Pl. 8). No other lateral-lines can be seen on the head or the trunk. The web of the right pelvic fin is seen in P.52441a (*pv.f*, Pl. 9, fig. 1). It is coated with rows of small scales which appear to be similar to the adjacent body scales. The other fins, including the caudal, are unknown.

The sculptured crowns of the flank scales do not recall closely any other genus (*V. uncinatus* is undescribed in this respect). They have a general resemblance, however, to the scales of *Nostolepis gracilis* figured by Gross (1947, Pl. 26, figs. 1–4). The larger body scales from the median dorsal region, shoulder-girdle and bases of the fin-spines are intermediate in sculpture between the flank scales and tesserae of the head. They are not unlike a figured scale of *N. robusta* (Brotzen), although they are more sparsely ornamented (Gross 1971, Pl. 6, fig. 17).

(iii) *Spines*. The relative lengths of the fin-spines are unknown, but they have been estimated for Text-fig. 16. None is deeply embedded in the body wall. The pectoral spine is less strongly arched than in *V. uncinatus*, and it lacks posterior denticles (*p.sp*, Pl. 1, fig. 1, Pls. 8, 9, fig. 2, Pl. 10). It is ornamented with at least 17 fine, beaded ridges on its dorsal and ventral surfaces. Near the anterior margin these ridges are more robust and have the typical climatiid noded ornamentation. The pelvic (*pv.sp*) and anal (*a.sp*) spines have a similar length and are ornamented with numerous fine beaded ridges; they are only slightly curved. The anterior dorsal spine is slightly curved and probably of similar length to the pectoral. It is probably longer than the posterior dorsal, which is almost straight. Both of the dorsal spines are ornamented with numerous fine, beaded ridges, which proximally dissolve into tubercles, as in the case of the pectoral spine. Of the six pairs of intermediate spines, the first (*isp1*, Text-fig. 14) is large and situated below the scapulocoracoid. The second (*isp2*) and sixth (*isp6*) are vestigial in P.24938a, b (Pl. 1, fig. 1, Pl. 8). In P.52441a, b, however, the sixth is well developed, and although it cannot be seen completely, the second also appears to be a large spine (Pl. 9, fig. 1, Pl. 10). Variation in the number of intermediate spines has been noted by Watson (1937 : 61, 65) in *Climatius reticulatus* and *Euthacanthus macnicoli*, and it may be a common phenomenon in climatioids, although it is worth stressing that it is often difficult to make an accurate count of these spines. Each intermediate spine is ornamented on both sides with about 13 beaded ridges, which converge on the tip.

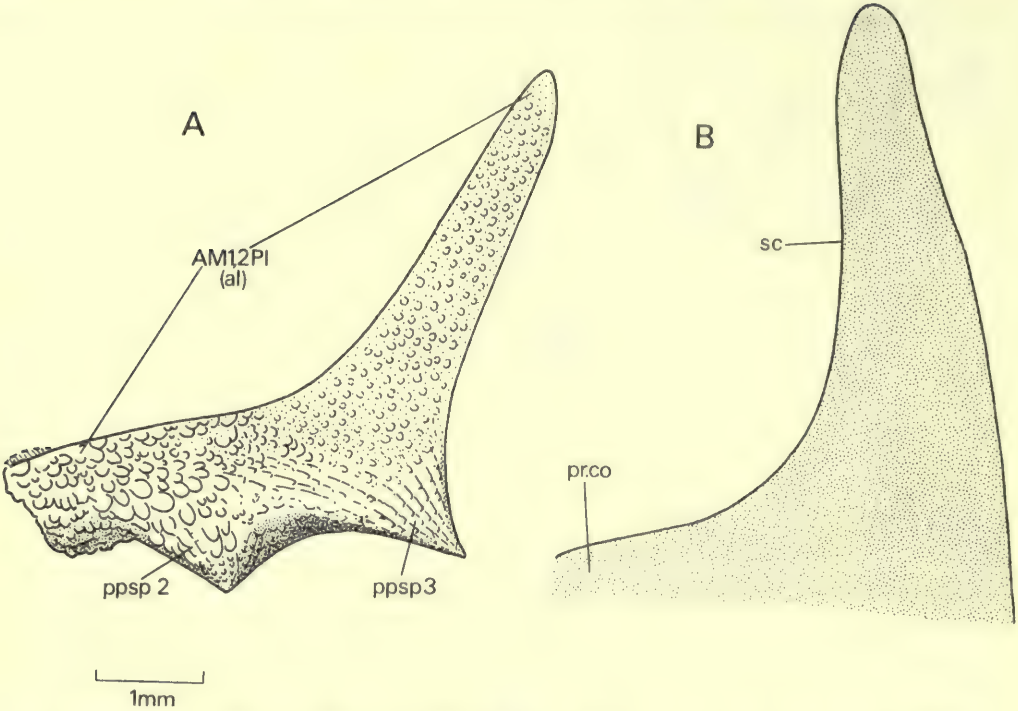
(iv) *Shoulder-girdle*. The dermal shoulder-girdle is represented by the paired ascending lamina (A*M1,2Pl*, Text-fig. 15A, Pl. 1, fig. 1, Pl. 10), which was situated in the postbranchial wall against the scapulocoracoid, and by a separate median ventral tessera (*ALo*, Text-fig. 14, Pl. 9, fig. 2). The ascending lamina bears two ventrolaterally-directed paired prepectoral spines (*ppsp2, ppsp3*). The homologies of these elements are discussed below (p. 180). There are no paired ventral plates. The areas between the median tessera and the various spines are filled by a mosaic of enlarged scales (Text-fig. 14, Pl. 9, fig. 2). The scapulocoracoid is covered on its lateral surface by closely applied, enlarged scales. In its general features this structure is like the scapulocoracoid of *V. uncinatus* (Text-fig. 33B), with a moderately broad scapular blade (*sc*, Text-fig. 15B) and a coracoid process (*pr.co*). The coracoid region is unknown.

The exact relationship of the dermal ascending lamina to the scapulocoracoid is unknown. However, its arched form matches that of the anterior margin of the



Text-fig. 14. *Vernicomacanthus waynensis* gen. et sp. nov. Lower Old Red Sandstone. Plan of ventral surface of the body in the region of the right shoulder-girdle. After holotype, BM P.24938. Ditton Series, Wayne Herbert quarry, Newton, Herefordshire, England.

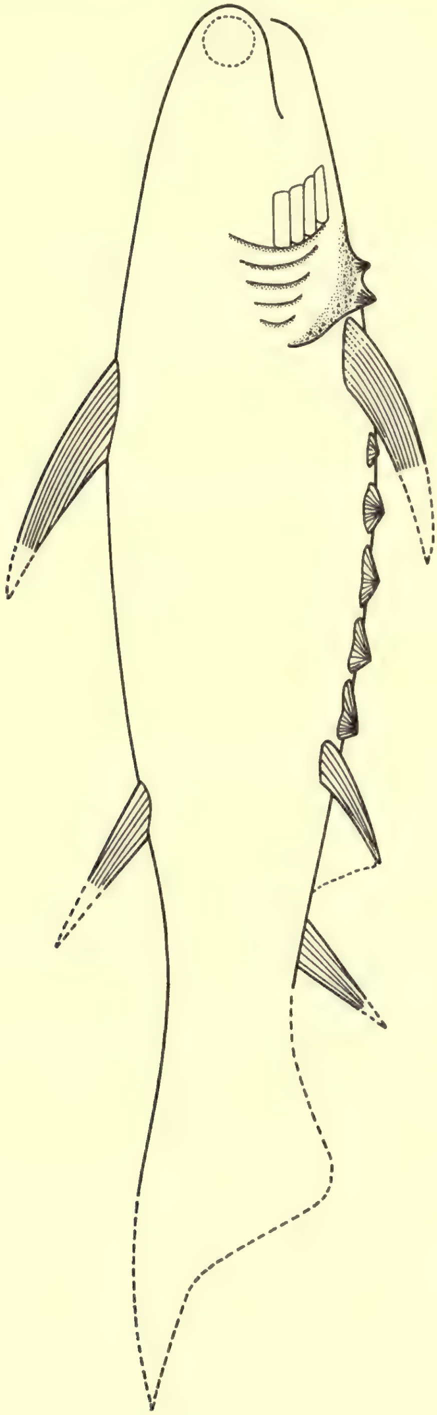
scapulocoracoid, and it seems likely that the dermal element was placed just in front of the scapula so that the coracoid process projected forwards mesially to the paired prepectoral spines. The posterior paired prepectoral spine (*ppsp3*) must have been carried immediately in front of the pectoral spine (Text-fig. 16). The ornamentation of flattened tubercles on the ascending lamina (Text-fig. 15A, Pl. 1, fig. 1, Pl. 10) supports this interpretation, as a similar ornamentation is found in comparable positions in more completely ossified climatiid shoulder-girdles (Text-fig. 29A).



Text-fig. 15. *Vernicomacanthus waynensis* gen. et sp. nov. Lower Old Red Sandstone. A, dermal shoulder-girdle, left, in lateral view. After BM P.17522. B, plan of scapulocoracoid, left, in lateral view. After holotype, BM P.24938. Ditton Series, Wayne Herbert quarry, Newton, Herefordshire, England.

(v) *Head*. The exoskeleton of the head is incompletely seen in P.24938a, b (Pl. 1, fig. 1, Pl. 9, fig. 2). It comprises tesserae stellatae (*tt.mt*) which show little regional variation, other than in their size. The largest elements are in the rostral and mandibular regions. The same specimen has a definite series of lower jaw teeth (*t*, Pl. 9, fig. 2). It is not known whether this species possessed upper jaw teeth. As in *Nostolepis* and *Ptomacanthus* the teeth are arched plates with three or four blade-like cusps, but unfortunately the details of their structure cannot be worked out. Their presence may indicate that *V. waynensis* is closely related to *Nostolepis* and *Ptomacanthus* (but see p. 200). If not, they weaken the evidence I have used to relate these last two genera (p. 139). Teeth are present in the lower jaw of *V. uncinatus*, but their detailed morphology is unknown. In P.52442 there are the remains of four spathiform branchiostegal rays, seen in visceral view. They have been restored diagrammatically in Text-fig. 16 (cf. *V. uncinatus*, Pl. 7).

Discussion. *V. uncinatus* and *V. waynensis* are undoubtedly similar fishes in their gross morphology, and they appear to be closely related. This conclusion is supported by a comparative study of the shoulder-girdle (*v. infra*), which also



TEXT-FIG. 16. *Vernicomacanthus waynensis* gen. et sp. nov. Lower Old Red Sandstone. Restoration in lateral view.

suggests a fairly close relationship between *Vernicomacanthus* and *Parexus*. Whether or not *V. uncinatus* and *V. waynensis* are congeneric is still an open question. However, *V. uncinatus* is quite distinct from *Climatius reticulatus*, and it seems better to include both *V. uncinatus* and *V. waynensis* in a single new genus, than arbitrarily create two new genera for these species, in our present inadequate state of knowledge.

Order ISCHNACANTHIFORMES

Family **ISCHNACANTHIDAE**

URANIACANTHUS gen. nov.

Etymology. *Urania*, Daughter of Oceanus and Tethys [Myth]; Gr. *akantha*, a thorn.

Definition. Ischnacanthiforms with two pairs of intermediate spines, and with the anterior dorsal fin-spine longer than the posterior dorsal.

Type species. *Uraniacanthus spinosus* sp. nov.

Remarks. The classification of this genus and the definitions of some ischnacanthid taxa are discussed below.

URANIACANTHUS SPINOSUS sp. nov.

Pl. 11–13

1956 (?) cf. *Diplacanthus;* Denison : 394

Etymology. L. *spinosus*, spinous.

Diagnosis. The sole species referred to the genus.

Type. The holotype is BM P.16609 (Pl. 11), a small individual with an almost complete trunk but lacking the head.

Horizon. Ditton Series, about 66 m above the main '*Psammosteus*' limestone, in the *Pteraspis crouchi* zone.

Locality. Wayne Herbert quarry, near Newton, SW. Herefordshire; in the siltstone lenticle described by White (1935 : 383).

Material. This account is based on six specimens in the BM; P.16609, the holotype; P.16610–1, the flank of a fish in part and counterpart (on the back of this block are a scapulocoracoid and pectoral spine referred to *Vernicomacanthus waynensis*, which have not been described, and an undetermined meckelian cartilage); P.16612–3, the head and pectoral region in part and counterpart (Pl. 13); P.20000–1, the posterior region of the body with well-preserved caudal, anal and posterior dorsal fins, in part and counterpart (Pl. 12) (P.20000 is on the same block as the type of *Ptomacanthus anglicus*, P.19999); P.53030–1, an incomplete, distorted trunk in part and counterpart; P.53032–5, a body wanting the tail and much of the head, but with associated jaws. A seventh specimen (P.16609) may belong to this species, but it is preserved as a poor impression and has not been considered.

DESCRIPTION. (i) *General features.* With the exception of the dorsally flattened head and shoulder-girdle in P.16612–3 (Pl. 13), the specimens are laterally compressed with the ventral wall tending to be turned in the same plane as the flank (Pl. 11). This suggests that the body was suboval in section with a broad venter between the paired fin-spines, and with a broad skull-roof. The holotype is estimated to have been about 80 mm long, but other specimens show that this species reached at least 150 mm. Measurements of fin-spines are given in Table 2, but the paucity of material and the problem of making accurate measurements preclude an estimate of the variation in their relative proportions. The spines are long and slender. The anterior dorsal (*ad.sp*) is longer than the posterior dorsal (*pd.sp*) and is situated just posterior to the shoulder-girdle. The pelvic spines (*pv.sp*) are inserted well in front, and the anal spine (*a.sp*) immediately in front, of the level of the posterior dorsal spine (*pd.sp*). There are two pairs of well-developed intermediate spines (*isp1*, *isp2*), with the anterior pair inserted between the pectoral spines (*p.sp*). There are neither median nor paired prepectoral spines, and no dermal plates in the shoulder-girdle.

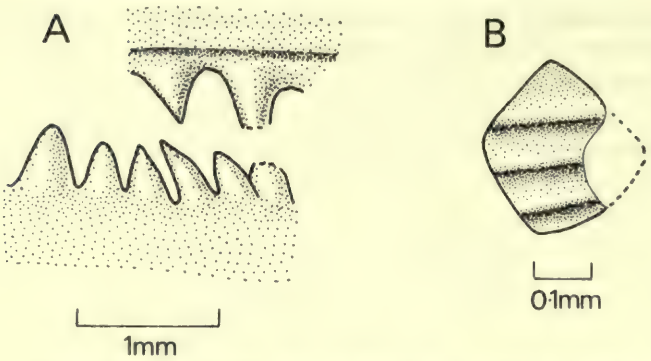
TABLE 2

Length (in millimetres) of exserted portion of fin-spines of *Uraniacanthus spinosus* gen. et sp. nov.

Specimen	Ant. dorsal	Post. dorsal	Pectoral	Pelvic	Anal
P.16609	24	14	—	12	15
P.16610–1	—	21	—	11	20
P.16612–3	—	—	Ca. 16	—	—
P.20000–1	—	28	—	—	33
P.53030–1	—	24	—	12	—
P.53032–5	32	—	—	—	—

(ii) *Squamation.* The small trunk scales are poorly seen in the specimens. They have a flat base and a moderately high, flat crown. The surface appears to be ornamented with three or four parallel or subparallel ridges, but the restoration in Text-fig. 17B is intended to show only the general character of the crown and it requires corroboration. There is little region variation, and there are no tesserae on the head. The scale crowns are, however, enlarged and further flattened mesial to the base of the pectoral fin, between the pectoral and first intermediate spines, at the bases of some of the other spines (e.g., the posterior dorsal, Pl. 12), and anterior to the first dorsal spine. The number of ridges increases to five or six on these enlarged crowns.

The webs of the median and paired fins are coated with rows of minute scales, and are unusually well preserved (*ad.f*, *pd.f*, *pv.f*, Pls. 11–13). There are no fin webs behind the intermediate spines. The caudal fin (Pls. 11, 12; Text-fig. 18) has scale zone 1 (*Z1*) distinctly developed in the usual way. Zone 2 (*Z2*) is also well differ-



Text-fig. 17. *Uraniacanthus spinosus* gen. et sp. nov. Lower Old Red Sandstone. A, upper and lower teeth from anterior region of jaws. Sketch of BM P.53032. B, sketch of crown of flank scale. After BM P.16613.

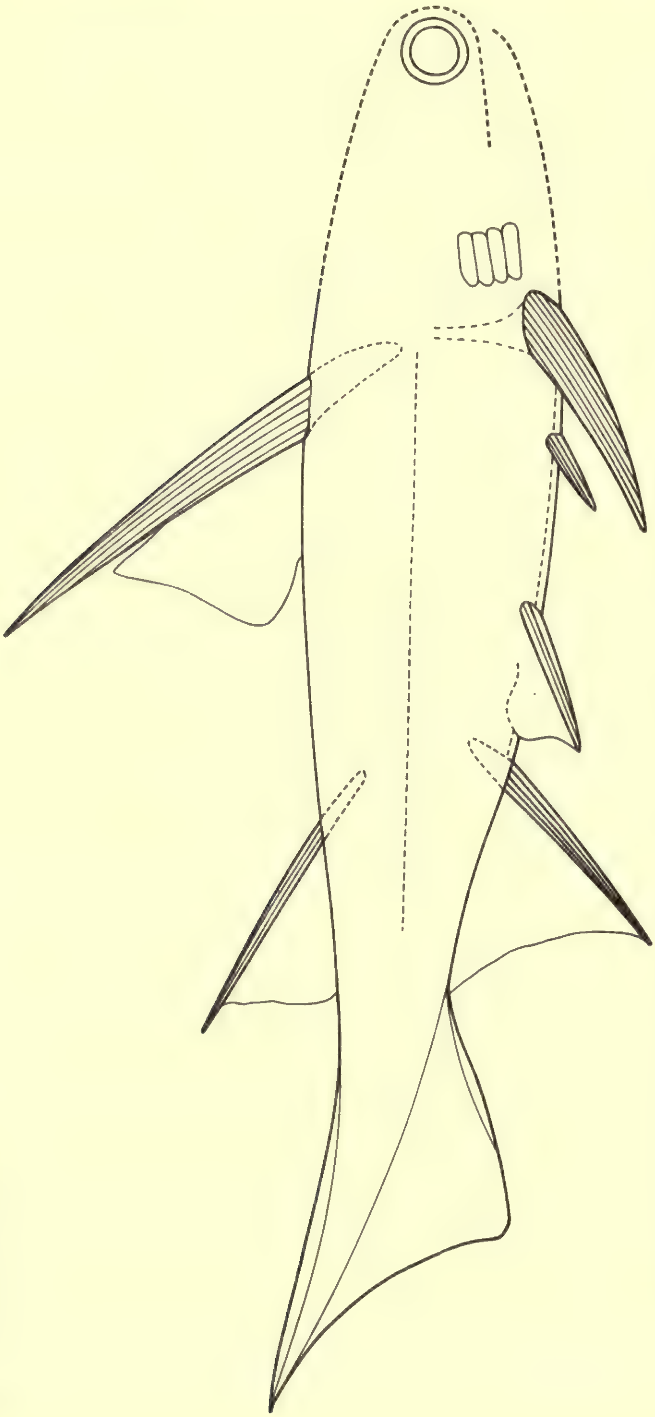
entiated, but as in *Ptomacanthus* it is not clearly subdivided into zones 2 and 2″. Enlarged scales along the margin of the fin may, however, represent zone 2″. The hypochordal lobe bears long rows of fine scales, comparable with those on the dorsal and anal fins (Pl. 12). They cannot be separated into zones 3 and 4, but a narrow band of enlarged scales along the leading edge of this lobe (Pl. 11) is comparable with zone 3″ of *Ptomacanthus*.

The main lateral-line can be observed to pass back between rows of flank scales in P.53030–1; and the ventral line can be seen in P.53035 running between rows of slightly enlarged scales mesial to the pectoral fin. The two lines are restored in Text-fig. 18 on the evidence of these specimens.

(iii) *Spines*. The median fin-spines are deeply inserted in the body muscles (Text-fig. 18, Pls. 11, 12), as they are in *Ischnacanthus gracilis* (Egerton) (Watson 1937, Text-fig. 10). The spines are devoid of nodes, except at the bases of the pectoral and anterior dorsal spines, and can thus be separated immediately from the spines of the other Wayne Herbert species. The number of smooth ridges at each side of the fin-spines near their bases is as follows: anterior dorsal, 8; posterior dorsal, 3 or 4; pectoral, about 8; pelvic, 6; anal, 4 or 5.

(iv) *Shoulder-girdle*. This is represented only by a perichondral scapular ossification (*sc*, Pl. 13, fig. 1; also P.53034), which is similar in its size and relations to that of *Ischnacanthus gracilis* (Text-fig. 18). The lack of dermal bones and prepectoral spines is a further notable difference between *U. spinosus* and the other Wayne Herbert species.

(v) *Head*. The squamation of the body continues forwards on to the head, with little change in character. Four spathiform branchiostegal rays are preserved in P.16612–3 (*br*, Pl. 13). They have an ornamentation of fine, subparallel and partly interconnected ridges. There are probably traces of the circumorbital ring in the same specimen. The jaw remains in P.53032 (Pl. 12, fig. 1) indicate that the palato-



Text-fig. 18. *Uraniacanthus spinosus* gen. et sp. nov. Lower Old Red Sandstone. Restoration in lateral view.

quadrate was low with an extrapalatoquadrate ridge, and that the meckelian cartilage had a deep fossa for the adductor muscles. They show no other details of the replacement bones, but the structures that are preserved are comparable with the corresponding regions of *Ischnacanthus gracilis*. Along the upper margin of the lower jaw, and anteriorly in the upper jaw (Text-fig. 17A), there are preserved single series of teeth firmly anchylosed to the adjacent bones. Each tooth is circular in section and without side cusps. A dental element is also seen in P.16612–3 (*dg.b*, Pl. 13); although it is small, displaced, and the details of its structure are indistinct, it is provisionally determined as a marginal jaw element showing three or four principal cusps and several rows of side-cusps. An alternative interpretation, in which I have almost equal confidence, is that it is a symphysial tooth similar to those figured for *Gomphonchus* (e.g. Gross 1957, Pl. 2). There is no sign of a dermal mandibular bone (i.e. a 'mandibular splint').

A more detailed description and discussion of these jaw elements is not warranted by their preservation. They are important, nevertheless, in establishing that *U. spinosus* is a tooth-bearing fish and that some of the teeth are fused into jaw bones.

Discussion. The presence of tall, deeply inserted dorsal fin-spines, and two pairs of well-developed intermediate spines gives *Uraniacanthus* a superficial resemblance to diplacanthoids. Although teeth are not known in this last group, their presence in *Uraniacanthus* does not seriously detract from this resemblance, because they are primitively present in climatiiforms and might reasonably be expected to occur in primitive diplacanthoids. However, *Uraniacanthus* does not have the large scapulocoracoid or the dermal shoulder-girdle plates that characterise diplacanthoids (p. 191). These are important differences, and I think they are sufficient to demonstrate that *Uraniacanthus* does not belong to this group.

Dentigerous jaw bones are found in both primitive climatiids (*Nostolepis*) and in ischnacanthiforms, and in most cases a detailed study is required before a species can be referred to one or other of these groups on the characters of these elements (e.g. Ørvig 1967). Such a study is not possible with the materials of *Uraniacanthus* now at hand, although it may be noted that the circular section of the teeth favours ischnacanthid affinities (Gross 1957 : 35; Ørvig 1967 : 146). If this evidence is allied with the complete lack of dermal structures in the shoulder-girdle, including prepectoral spines, and the deep insertion of the dorsal and anal fin-spines (which would be unusual in a climatioid carrying dentigerous jaw-bones), it seems evident that *Uraniacanthus* is an ischnacanthiform.

The only other articulated ischnacanthiform is *Ischnacanthus gracilis* from the Lower Old Red Sandstone of Scotland. *Uraniacanthus* differs from this species most notably in the presence of intermediate spines and sculptured scale crowns. In both of these characters *Uraniacanthus* is doubtless more primitive than its Scottish relative.

One result of the description of *Uraniacanthus* is that my definition of the order Ischnacanthiformes (Miles 1966 : 166) now needs to be amended. The words 'no intermediate spines' should be removed from this definition, and I feel it is also advisable to omit the following statements, as it is not known how widely they apply within the group; 'and bearing *Poracanthodes*-type scales along some of the cephalic lateral-lines'; 'a large gill-cover covering the whole of the gill-chamber laterally'; 'symphysial tooth whorl in lower jaw and other tooth whorls in the mouth cavity'. Ischnacanthiforms can be described as acanthodians with dentigerous jaw-bones in both the upper and lower jaws, with two dorsal fins, and without dermal plates and prepectoral spines in the shoulder-girdle.

I have provisionally referred *Uraniacanthus* to the Ischnacanthidae (with the same definition as the Order), as this is the only formally recognised family of ischnacanthiforms, and there is insufficient evidence for a proper discussion of the relations of the genus within the order. Ørvig (1967 : 145; cf. Miles 1966 : 166) has excluded *Acanthodopsis* and *Atopacanthus* from the ischnacanthids, but has yet to publish his revised classification. This exclusion is based on jaw structure and it seems a reasonable step; Ørvig's full results are awaited with interest. Finally I have no reason to suppose that *U. spinosus* is conspecific with *Ischnacanthus kingi* White, *I. wickhami* White, *I.* (?) *anglicus* White, *Onchus wheathillensis* White or *'O.' besomensis* White (1961), all from the English Dittonian.

III. THE STRUCTURE OF ACANTHODIAN SHOULDER-GIRDLES

Order ACANTHODIFORMES

Family **ACANTHODIDAE**

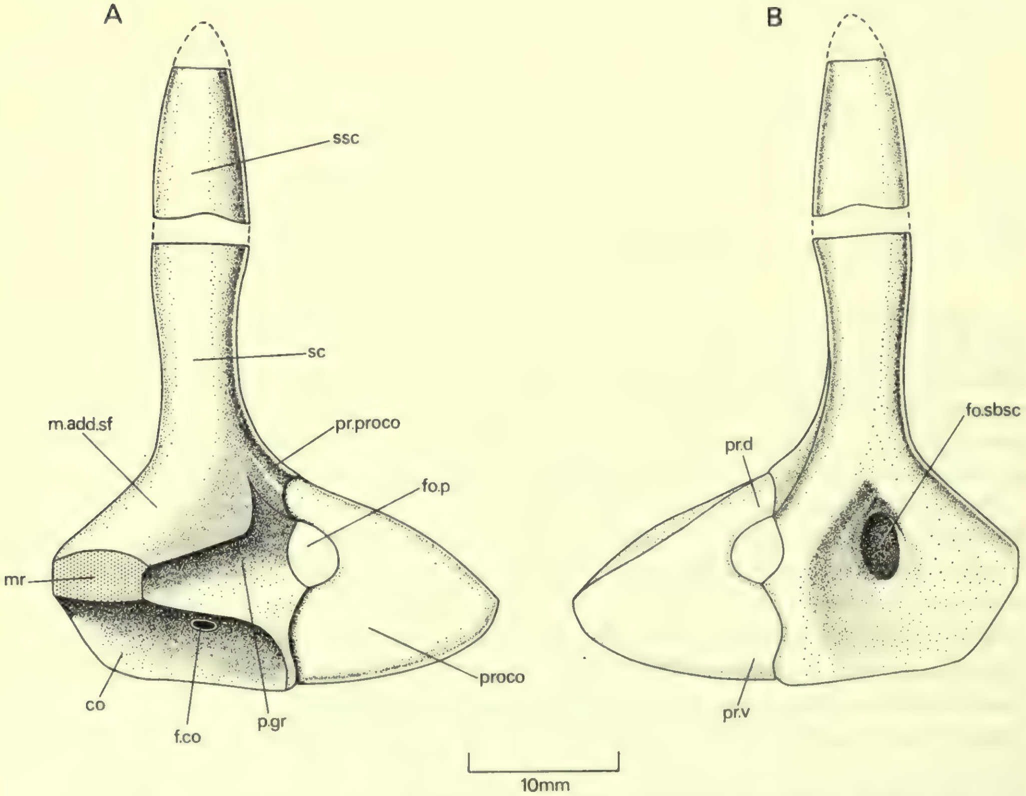
ACANTHODES BRONNI Agassiz

Three authors have described the endoskeletal shoulder-girdle of this species. The first, Reis (1890, Text-fig. 7; 1895, Pl. 6, figs. 11–13), by virtue of his extraordinary interpretation, seems to have gained no clear idea of its structure. The second, Jaekel (1899, Text-fig. 2), produced a brief account which is accurate in most respects, as far as it goes. The third, Watson (1937, Text-figs. 20–22), gave an incomplete account, inferior to the work of Jaekel, to which he did not refer.

The following account, like these earlier works, is based on specimens from the Lower Permian of Lebach, Germany. The negatively prepared specimen in the Berlin collection used by Jaekel is now unfortunately lost, but a cast from this specimen is preserved (HU MB24, copy BM P.49991), and another specimen (HU MB14, cast BM P.49980) confirms all the major points of structure (Pl. 14, figs. 1, 2).

Endoskeletal girdle. The girdle (Text-figs. 19, 20) comprises three separate perichondral ossifications, the scapulocoracoid, suprascapula (*ssc*) and procoracoid (*proco*), which have no contact with their fellows of the other side. The terms suprascapula and procoracoid were applied by Jaekel, and the objection might be raised that it is wrong to use names from bony fishes and tetrapods for ossifications in the girdle of acanthodians. However, terms such as scapula and coracoid have long been applied to ossifications in the primary girdle of different groups of vertebrates without undue confusion, even though these ossifications may not be properly homologous throughout. It is in the same spirit that the terms suprascapula and procoracoid are retained in acanthodians (cf. Dean 1907 : 217). We may orientate the girdle of *Acanthodes* by assuming that the scapular blade (*sc*) stood vertically in the body, and that the procoracoid was directed anteromesially.

The scapulocoracoid has a stout middle region, which is surmounted by a slender scapular blade (*sc*), and is continued ventrally by the coracoid plate (*co*). Posterolaterally the middle region is produced into a horizontal margo radialis (*mr*) for the articulation of the pectoral fin skeleton. Unfortunately the details of this surface cannot be observed. Anteromesially at the same level, the middle region bears a deep groove for the pectoral spine (*p.gr*). The base of the scapular blade descends to the upper edges of the margo radialis and the pectoral spine groove, in a smooth sweep of bone which may be compared with the supraglenoid buttress of primitive



TEXT-FIG. 19. *Acanthodes bronni* Agassiz. Lower Permian. Restoration of shoulder-girdle in A, lateral and B, mesial view. After cast BM P.49991; original from Lebach, Germany.

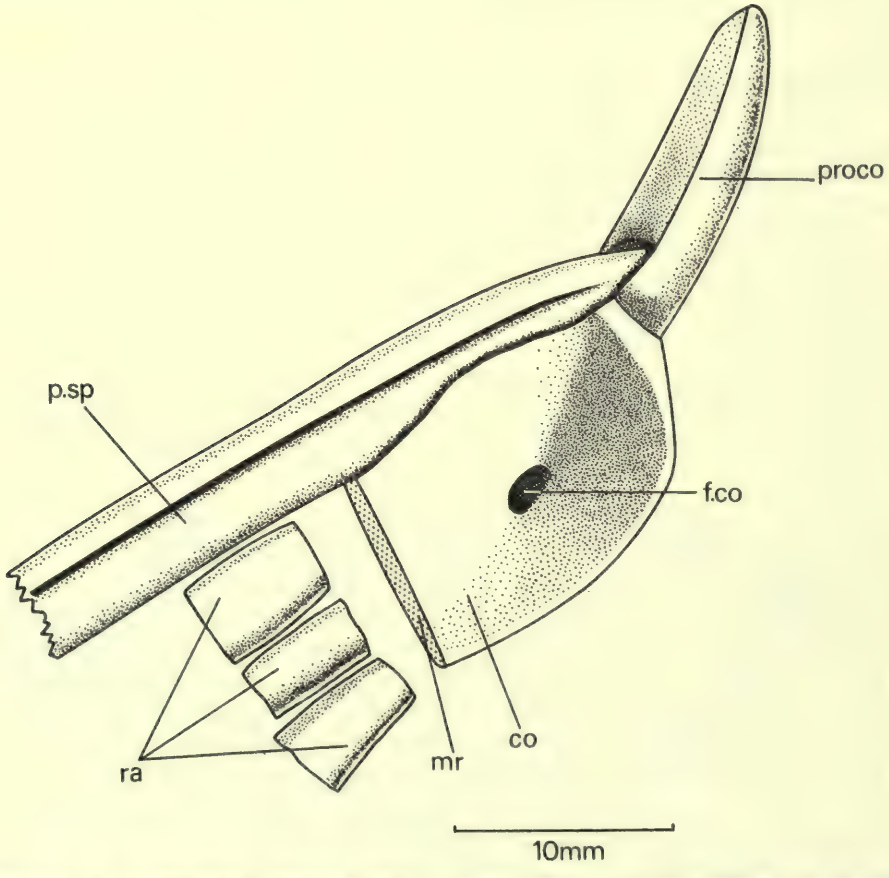
tetrapods and bony fishes (Romer 1924; Andrews & Westoll 1970). The resulting surface (*m.add.sf*) gave origin to the dorsal adductor muscles of the fin. The tip of the scapular blade lacks a perichondral cover, and was presumably connected to the suprascapular by cartilage; the girdle is nearly circular in transverse section at this point (Watson 1937 : 113). Anterolaterally the base of the scapular blade is produced into a procoracoid process (*pr.proco*) over the anterior region of the pectoral spine groove. The terminal face of this process is concave, and lined with endochondral bone.

Below the middle region of the scapulocoracoid, the coracoid plate is hollowed out laterally into an extensive fossa for the origin of the ventral abductor muscles. This fossa is bounded anteriorly by a stout vertical ridge whose anterior face is slightly hollowed into an articular face for the procoracoid. The mesial face of the scapulocoracoid (Text-fig. 19B) is broken by a large subscapular fossa (*fo.sbsc*), which leads to a coracoid foramen (*f.co*) in the ventral muscle fossa. This foramen transmitted diazonal nerves, and possibly blood vessels as well, to the ventral surface of the fin.

The procoracoid (*proco*, Text-figs. 19, 20) is a thin plate standing vertically in the body. The details of its lateral surface are not well known, but probably it lacked prominent features, as does the mesial surface. Posterodorsally it is produced into a narrow process (*pr.d*) of circular cross-section, which articulated against the procoracoid process of the scapulocoracoid; and posteroventrally it is produced into a thicker, deep process (*pr.v*), which abutted against the anterior articular face of the coracoid plate. As a result, superior and inferior articulations may be recognised between the procoracoid and the scapulocoracoid. Between these two articulations, the embayed posterior margin of the procoracoid and the anterior margin of the scapulocoracoid enclose a large pectoral fossa (*fo.p*), which received the head of the pectoral spine (Text-fig. 20). The suprascapula (*ssc*) shows no special features. It lacks perichondral bone both dorsally and ventrally, and was presumably capped with cartilage.

PECTORAL FIN. When the pectoral spine is in place in the groove on the scapulocoracoid, it slopes posterolaterally to enclose an angle of about 60° with the rostrocaudal axis, and inclines ventrally at some 10° from the horizontal. The pectoral fin skeleton of three stout elements which articulate against the margo radialis (*ra*, Text-fig. 20) is well seen in numerous specimens (Pl. 14, figs. 1, 2; Reis 1895, Pl. 6, fig. 11; 1896, Pl. 1, figs. 2, 5, Pl. 2, fig. 4, Pl. 3, fig. 3; Jaekel 1899, fig. 2), and was normally perichondrally ossified (cf. Watson 1937 : 114). A further feature, well seen in many specimens, is the position of the fin-rays ('ceratotrichia', see Miles 1970), which proximally overlie the distal ends of these fin elements.

Watson (1937 : 114, Text-fig. 22) has suggested that there was a second, more distal series of elements in the fin base, and he interprets the endoskeleton as 'tribasal, of general Elasmobranch character', with both basal and radial series, although he finds that 'it is not possible to be sure of the structure'. The photograph of Watson's (1937, Pl. 13, fig. 5) specimen suggests, however, that his 'radial' could be a proximal element of the left fin, whilst his 'pro-', 'meso-' and 'metapterygial' elements are clearly the proximal elements of the right fin. The evidence for Watson's radial series is thus poor, and is not corroborated by other specimens. I suggest, therefore, that the contact between the proximal ends of the fin-rays and the three endoskeletal elements indicates the absence in life of an extensive distal series of elements of the type reconstructed by Watson, and that the three ossified elements of the fin should properly be interpreted as radials. It is of course possible that there was a second short series of radials, unossified, such as found in *Pteronisculus* (Nielsen 1942, Text-fig. 51) and *Acipenser* (Jessen 1968, Text-fig. 8B). If the equivalent of a basal series is to be sought in *Acanthodes*, it may best be looked for as an undifferentiated area in the region of the scapulocoracoid that carries the margo radialis. Like the basal series of primitive elasmobranchs, this region is situated



TEXT-FIG. 20. *Acanthodes bronni* Agassiz. Lower Permian. Restoration of shoulder-girdle and pectoral fin skeleton in ventral view. After cast BM P.49991; original from Lebach, Germany.

proximally to the radials and is in the body wall (cf. *arthrodires*, Miles & Westoll 1968 : 444–445).

Thus the pectoral fin of *Acanthodes* had an articulation with the scapulocoracoid of moderate length; it had a small muscular lobe with three stout, ossified radials; it was aplesodic (Jarvik 1959 : 14); and it had an extensive web which was stiffened with a dorsal and a ventral series of fin-rays. These fin-rays have been described by Watson (1937 : 114). They were usually ossified only most proximally, although there is evidence from the most favourably preserved specimens that they extended to the edge of the fin. Watson notes that each series of 'ceratotrichia' may be folded on itself in laterally compressed specimens, and suggests that this indicates that 'the inner margin of the fin was attached to the body near the ventral surface for a long distance'. But this conclusion conflicts with the evidence from the moderate length of the fin articulation, and it is more likely that the condition results from the ventral deflection of the mesial region of the web, as seen, for example, in sharks and *Acipenser* (Jarvik 1965 : 161, Text-figs. 4A, B, 5E, 8D). Finally, in some specimens, the base of the fin was covered by small scales with a radial arrangement (Watson 1937 : 114), although this condition is better seen in some geologically older acanthodians (e.g. Pl. 15, fig. 1).

Watson (1937 : 114) records that 'the fin spines can be erected so that the two make an angle of 130° with one another'. This is substantiated by the new results presented above, particularly by the moveable joints between the procoracoid and scapulocoracoid. It is still not clear, however, whether the spine was lifted out of the groove, or whether the scapulocoracoid rotated in the body. The second mechanism would explain the cylindrical form of the scapula and the joint with the procoracoid, but would be unusual in comparison with modern fishes (sturgeons, catfishes). There is, however, no evidence of muscles specially developed to move the spine, which might have inserted on the procoracoid, and it is unlikely that muscles inserted directly on the smooth surface of the spine itself. In sturgeons, the pectoral spine (fused lepidotrichia) is attached to the first radial, which articulates with the girdle (Goodrich 1909 : 319, Text-fig. 279). Although there is no indication that the spine was attached to the first radial in *Acanthodes*, it seems likely that it was pushed forward by the fin. Thus it was erected as the web was spread by the operation of anterior erector slips of the dorsal and ventral fin muscles (with antagonistic posterior slips), originating on the scapulocoracoid (or on the procoracoid if the scapulocoracoid rotated with the spine). There is no sign of a mechanism to lock the spine in the erect position (see p. 207).

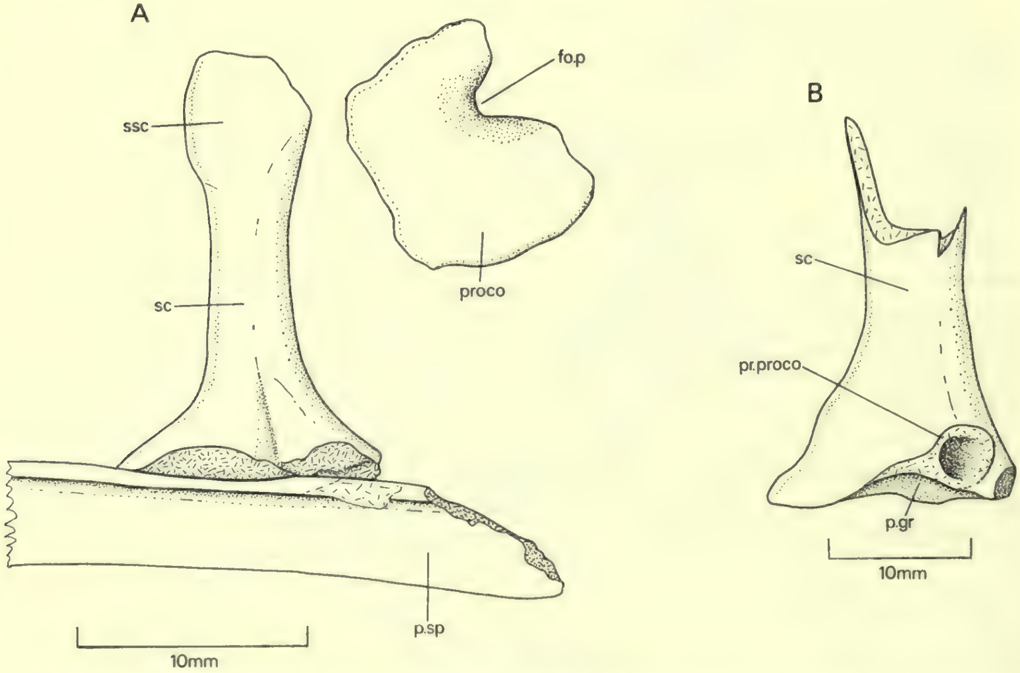
Acanthodes **spp.**

Certain other species of *Acanthodes* can be shown to resemble *A. bronni* closely in the structure of the pectoral girdle and fin, and this is presumably true of all properly determined species of the genus.

Fritsch (1895, Text-figs. 261, 263, 270) has figured a possible procoracoid ('Infraclavicula') in contact with a scapula ('Clavicula') of unexceptional form in the Lower Permian species *A. gracilis* (Beyrich). The shape of the procoracoid in his drawings suggests, however, some misinterpretation of the specimens.

Davis (1894 : 255, pl. 28, figs. 4, 5) has figured the scapula in the Upper Carboniferous *A. wardi* Egerton, and shown that it bears the same relationship to the pectoral spine as in *A. bronni*. One of his specimens (Text-fig. 21A) shows the procoracoid (*proco*), which is apparently closer in structure to that of *A. bronni* than is the procoracoid of *A. gracilis*. The swollen top of the scapulocoracoid in this specimen indicates that the suprascapula (*ssc*) is co-ossified with the scapular blade (*sc*). The similarities to *A. bronni* are confirmed and extended by another right scapula of *A. wardi* (Text-fig. 21B), which exhibits a distinct procoracoid process (*pr.proco*) and the upper part of the pectoral fin-spine groove (*p.gr*).

Since the above was written, Mr Steen R. Jensen (Copenhagen) has drawn my attention to the procoracoid of *A. nitidus* Woodward, from the Calciferous Sandstone Measures of Glencartholm, Scotland (BM P.20438). This element and the associated scapular blade have the expected form for a species of *Acanthodes*.



TEXT-FIG. 21. *Acanthodes wardi* Egerton. Upper Carboniferous. A, sketch of shoulder-girdle, BM P.8058, Knowles Ironstone Shale, Fenton, Staffordshire, England. B, sketch of scapula, BM P.8435, Upper Coal Measures, Collyhurst, Bradford, nr. Manchester, England.

Family **CHEIRACANTHIDAE**

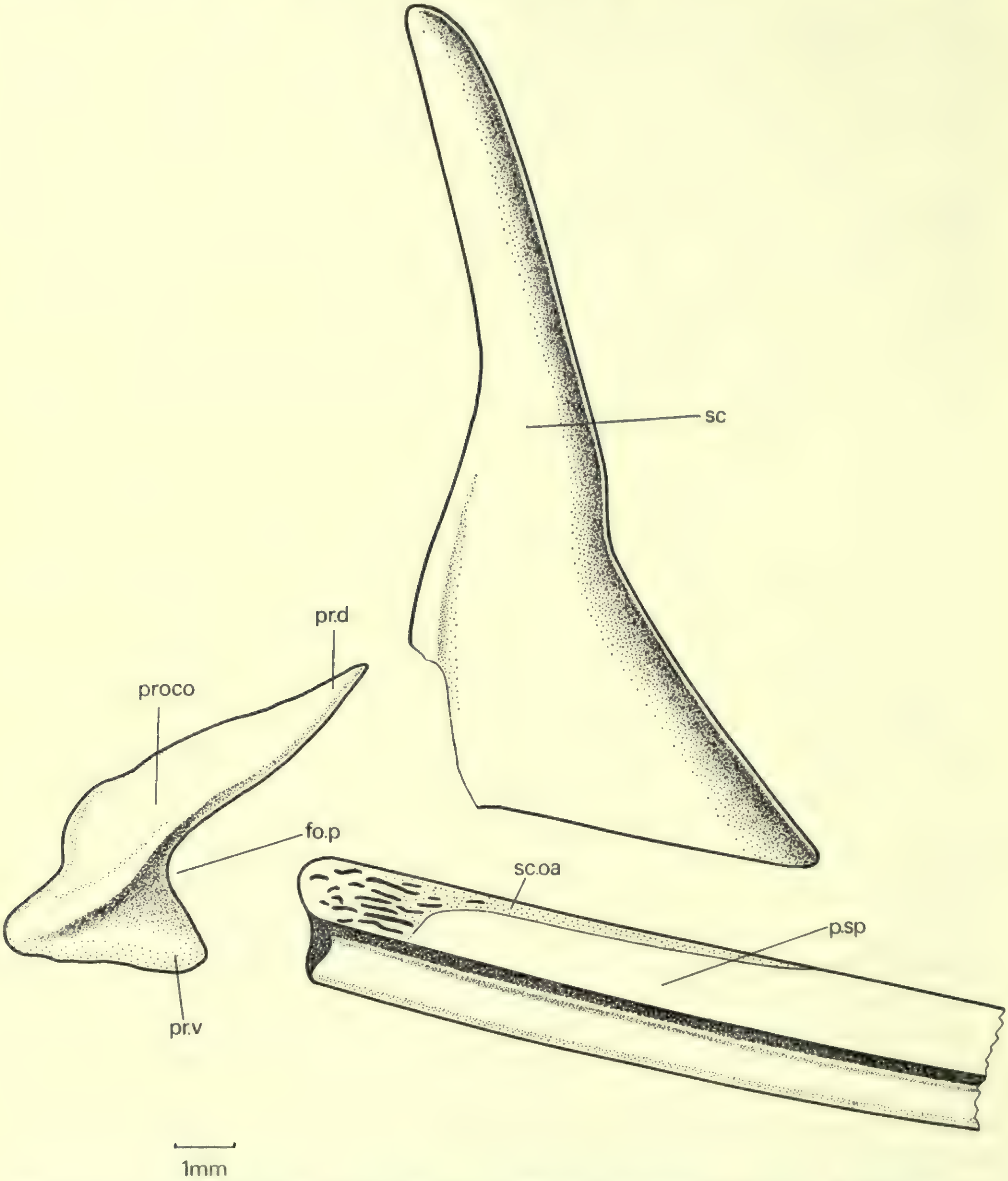
Cheiracanthus spp.

This account is based on specimens of *Cheiracanthus latus* Egerton and *C. murchisoni* Agassiz from the Moray Firth nodule beds in the Middle Old Red Sandstone of Scotland. Scores of specimens are preserved in the BM and the RSM. Watson (1937 : 84) remarks that these species 'are identical in their morphology but differ in proportions and in some details'. I am not sure that this is true with respect to the gill-covers, but the shoulder-girdles are closely similar in structure.

ENDOSKELETAL GIRDLE. The shoulder-girdle is well seen in specimens of *C. latus*, notably BM 34052, 36010 and RSM 1877.30.2 (also *Cheiracanthus* sp., RSM 1968.19.18 and RSM Kinnaird 168). The scapular region is perichondrally ossified except in its anteroventral corner, but there is no sign of the middle and coracoid plate regions, which must have been cartilaginous (Text-fig. 22, Pl. 15, fig. 2). The scapular blade (*sc*) apparently leaned slightly forwards in the body (Watson 1937, Text-figs. 12, 13) and has a circular cross-section. It includes the separate suprascapular of *Acanthodes bronni*. Ventrally the scapular blade is plate-like, and its outer surface ends in an almost straight lower edge which was in contact with the pectoral spine (*p.sp*). Thus it formed the upper border of a pectoral spine groove. The region in which one might expect to see the procoracoid process is not ossified, so it is not known whether this structure was present, although the form of the surrounding regions of the scapula suggest that it was. There is no indication of the margo radialis, and the mesial face of the scapula shows no important features, except in BM 36010 where it appears to include the upper part of a small subscapular fossa.

The procoracoid (*proco*) is a thin, vertically standing plate of perichondral bone ('coracoid', Watson 1937), closely comparable with that of *Acanthodes*. It is provided with a posterodorsal (*pr.d*) and a posteroventral (*pr.v*) process for superior and inferior articulation with the scapulocoracoid, but the nature of these articulations and the exact orientation of the element cannot be determined. Between these processes the posterior margin is embayed, which indicates the existence of a pectoral fossa (*fo.p*) for the head of the pectoral spine. The lateral face is marked by an oblique ridge and a slight depression in front of the posterior embayment.

PECTORAL FIN. The dermal pectoral spine is well known (Watson 1937). Proximally its leading face is marked by a narrow dorsal area (*sc.oa*, Text-fig. 22) which was overlain by the lower edge of the scapular ossification. This area gives way to a more coarsely textured area which was deeply inserted in the body wall. The relationship of the spine to the scapulocoracoid and its orientation in the body seem to have been very much as in *Acanthodes*, although the spine was probably less mobile than in this genus. Watson (1937) apparently erred in showing the spine detached from the scapula in his reconstruction. The endoskeleton of the fin is unknown, but the disposition of the fin-rays indicates that there was a small muscular lobe with short radials. The 'ceratotrichia' are particularly well seen in a specimen of *C. murchisoni* (Pl. 20, fig. 2). They are long, slender, unjointed rods in separate dorsal and ventral series, which reach well out towards the margins of the extensive web. They compare well with the 'ceratotrichia' of *Ischnacanthus gracilis* (Egerton) (Miles 1970, Text-fig. 8).



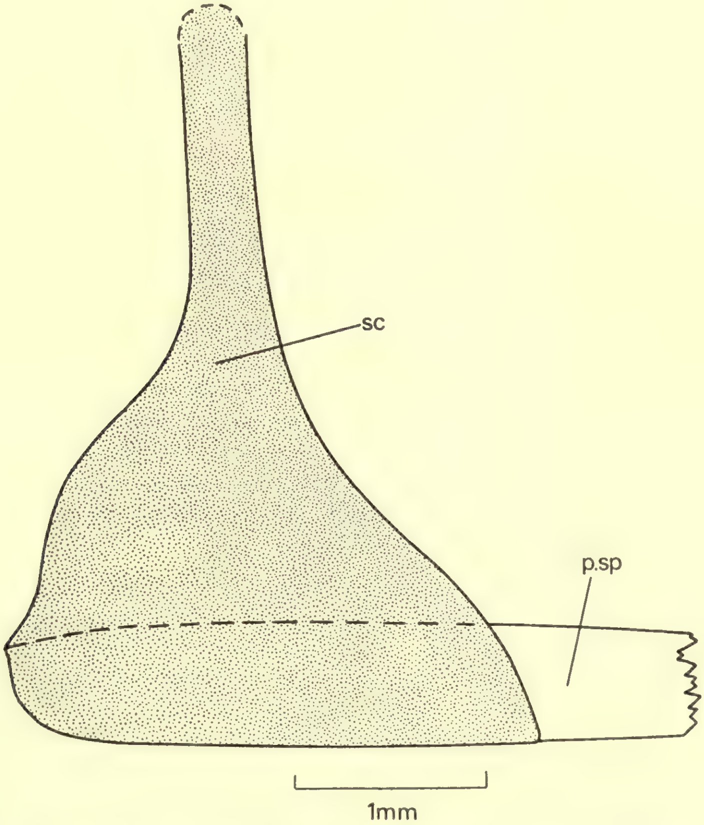
Text-fig. 22. *Cheiracanthus latus* Egerton. Middle Old Red Sandstone. Restoration of shoulder-girdle with bones shown slightly apart, in lateral view. Mainly after BM 35052, Tynet Burn, Banffshire, Scotland.

Family MESACANTHIDAE

Mesacanthus mitchelli (Egerton)

The shoulder-girdle and pectoral spine can be seen in many specimens from the Lower Old Red Sandstone of Angus, Scotland. I have examined the collections in the British Museum (Nat. Hist.) and the Royal Scottish Museum. Unfortunately the shoulder-girdle is usually poorly preserved, and in some respects it is difficult to interpret.

ENDOSKELETAL GIRDLE. Watson (1937 : 76, Text-figs. 8, 9) has described the salient features and it is only necessary to discuss some points which are open to a new interpretation. The following remarks are based mostly on BM 38594, P.7002 and P.1331. The perichondrally ossified girdle comprises the scapular blade (*sc*) and part of the middle region. The ossification spreads down inside the admesial



TEXT-FIG. 23. *Mesacanthus mitchelli* (Egerton). Lower Old Red Sandstone. Restoration of shoulder-girdle, in mesial view. After BM 38594, P.1331, P.7002, Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

face of the pectoral spine (Text-fig. 23). It is likely, therefore, that the spine was lodged in a groove on the outer face of the scapulocoracoid, although this cannot be confirmed with the specimens at hand. Watson records that the 'lower part of the bone has an ornamented surface as if it had a series of large overlapping scales fused on to it'. However, this 'ornamentation' is found on both the lateral and mesial surfaces and seems to be the result of post-mortem changes in the perichondral bone; it has a quite different appearance from the ornamented dermal bone found in the shoulder-girdle of contemporary climatiiform acanthodians. It is, therefore, not evident that dermal bone is included in the make-up of the girdle in *Mesacanthus*, and it seems unlikely that the surface of the girdle was exposed on the flank as Watson supposed. The scapula shows no sign of a procoracoid process. This may be due to poor preservation, but it seems more likely that this structure was absent. A procoracoid ossification has also not been recorded. This may be because (1) it has not been recognised in the specimens; (2) it was a separate element but is not ossified; (3) it was included in (co-ossified with) the scapulocoracoid, and therefore had no separate existence. It seems that explanation (2) or (3) is likely to be correct, but there is not yet enough evidence to decide between them. Nothing is known of the margo radialis.

PECTORAL FIN. It is unnecessary to add to earlier descriptions of the fin-spine, and the skeleton of the fin is not preserved.

Order ISCHNACANTHIFORMES

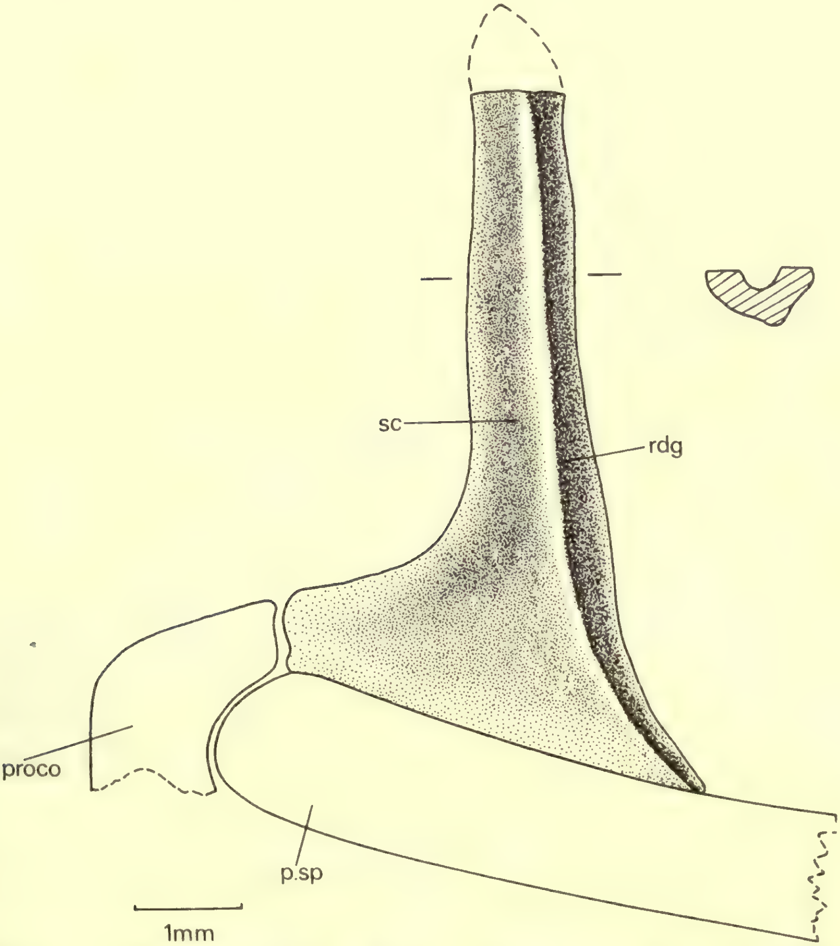
Family **ISCHNACANTHIDAE**

Ischnacanthus gracilis (Egerton)

I. gracilis is the only ischnacanthiform in which the pectoral fin and shoulder-girdle are adequately known. It is represented by many specimens from the Lower Old Red Sandstone of Scotland, and I have examined the large collections in the BM and the RSM. Unfortunately, as in the case of *Mesacanthus mitchelli* from the same beds, the details of the girdle and fin are difficult to interpret with any degree of certainty.

ENDOSKELETAL GIRDLE. The shoulder-girdle (Text-fig. 24) is represented by a scapular ossification (*sc*) of about the same extent as in *Mesacanthus*, although its mesial wall is incompletely ossified. Watson's (1937, Text-figs. 10, 11) drawings of this structure are accurate and he shows it in its correct relationship to the pectoral spine. However, he incorrectly concluded that it was partly dermal in origin, and this led him to the further incorrect conclusion that its inner face lay in contact with a cartilaginous scapula. To my mind there can be no doubt that the structure preserved in the fossils is of perichondral origin, and therefore properly termed the scapula. This is supported by two observations made by Watson (1937 : 81): (1) this structure was covered by ordinary body scales, (2) it is devoid of ornamentation.

The outer surface of the scapula (Text-fig. 24) is angled, so that it presents antero- and posterolateral faces which are sometimes separated by a low ridge (*rdg*). The anterolateral face may have formed a posterior wall to the gill-chamber, whilst the posterolateral face seems to have descended to a well-formed margo radialis. Several specimens (e.g. BM 46305c, d) give evidence of an incompletely ossified procoracoid (*proco*, Text-fig. 24). This element is closely comparable with the procoracoid of acanthodiforms, and appears to have had similar relations to the pectoral spine and scapula. However, as in the case of *Cheiracanthus*, there is no sign of a procoracoid process of the scapula.



TEXT-FIG. 24. *Ischnacanthus gracilis* (Egerton). Lower Old Red Sandstone. Restoration of shoulder-girdle in lateral view. After RSM Mitchell collection 86; BM P.9203, 46305c, d. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

Pectoral fin. Watson recorded the presence of four endoskeletal elements in the pectoral fin (RSM 1891.92.258). These may now be interpreted as radials by comparison with *Acanthodes bronni*. As in this last species, the 'ceratotrichia' radiate from the distal ends of these elements. These fin-rays have recently been redescribed (Miles 1970, Text-fig. 8). BM P.9118 shows that the web of the fin was coated with small scales running in long, radiating rows.

Order CLIMATIIFORMES

The shoulder-girdle of climatiiforms is characterised by the possession of ventral dermal plates. These plates are probably not homologous with the bones of the osteichthyan shoulder-girdle (see p. 205), although they may occupy more or less the positions of the cleithrum, the clavicle and the interclavicle. Hitherto a series of simple topographical names has been applied to them, such as 'anterior lateral plate', 'median ventral plate' and 'ventrolateral plate' (Watson 1937; Ørvig 1967). Unfortunately this terminology has not always been used accurately, and for my purposes it has proved to be inadequate for a proper discussion of the structure and evolution of the girdle. Another disadvantage is that it is similar to the terminology applied to the plates of the trunk-shield in placoderms, in which group acanthodians have been classified (e.g. Moy-Thomas 1939), although these fishes are no longer thought to be closely related (Miles 1965). There is little possibility that the dermal plates of acanthodians and placoderms are homologous. For these reasons I have found it necessary to introduce a new terminology for the plates in acanthodians, and this is done in the account of *Climatius reticulatus*. The compound plate names used in the descriptions of some species should be taken to imply (necessarily somewhat vague) topographic correspondence only. It is not possible to use a more precise terminology, based securely on the evolution of the plates, because there is no evidence to reveal with any certainty the primitive condition of the climatioid girdle (pp. 195–200).

Dean (1907 : 215) has asserted that the fins of acanthodians are 'beyond peradventure of a lateral fin-fold type', and this view has persisted to the present day to find expression most recently in the terminology applied by Ørvig (1967) to the prepectoral spines. Despite Dean's assertion, it seems that the fin-fold theory in its more naïve form has nothing to contribute to the study of acanthodians (Westoll 1958; Miles 1970 : 356), and this view is reflected in the terminology given below to the spines.

Suborder CLIMATIOIDEI

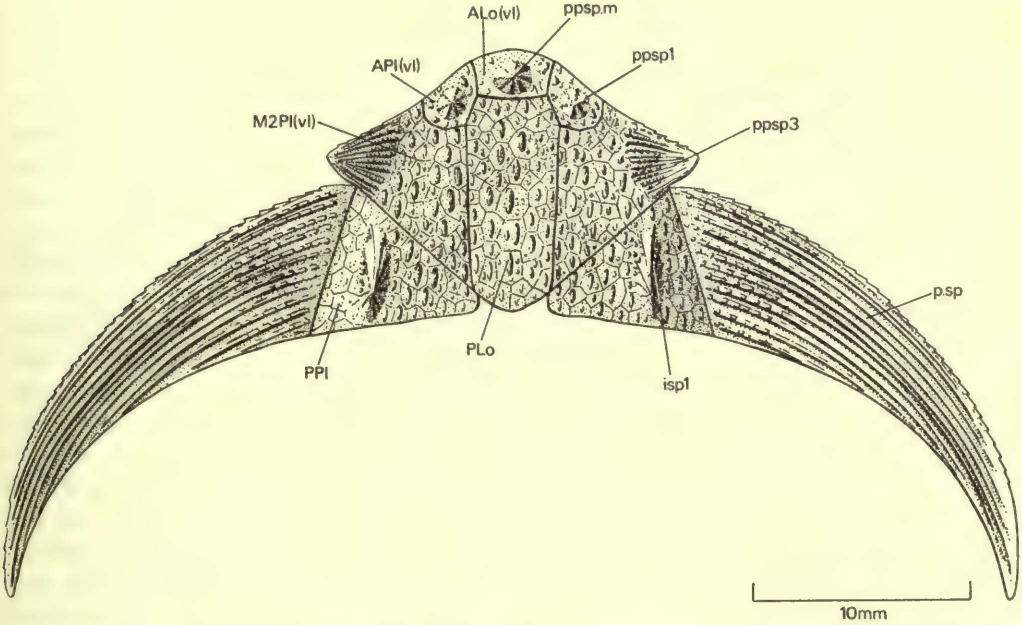
Family **CLIMATIIDAE**

Climatius reticulatus Agassiz

The shoulder-girdle of this species was first described by Watson (1937), and later by Ørvig (1967) who corrected a number of serious mistakes in the original account.

However, a fully accurate description remains to be given. The following account is based on specimens in the British Museum (Nat. Hist.), the Royal Scottish Museum and GSM 49785, all from the Lower Old Red Sandstone of Scotland.

DERMAL SKELETON. The dermal plates are in two series (Text-figs. 25, 26), a paired lateral series of three pinnal plates (*APl, M2Pl, PPl*) and a median series of two lorical plates (*ALo, PLo*). All but the posterior lorical plate are related to a spine of the intermediate-prepectoral series, and lateral to this spine series lies the pectoral spine (*p.sp*), which is attached to the posterior pinnal plate. Watson's (1937 : 60) account speaks of 'an area of tightly interlocked small bones' mesial to the base of the pectoral spine, whilst Ørvig (1967 : 137) affirms that the plates in this region are ornamented bones. The true condition of the dermal skeleton is clearly revealed by a number of specimens (Pls 3, 16, fig. 2), which show that the major plates of the girdle are thin, deeply-seated laminae of bone, and that these are overlain by mosaics of small polygonal scale-like bones. It seems probable that the plates comprise the fused basal layers of scales, and that the small bones are the free crowns of these scales (p. 198; cf. *Nostolepis*, Gross 1971), although the presence of entire, discrete scales is a preclimatioid condition. The ornamentation of the plates and spines is shown in the photographs (also Ørvig 1967) and will not be described further. The mutual relations of the spines and plates can be seen in the restorations (Text-figs. 10, 25, 26).



TEXT-FIG. 25. *Climatius reticulatus* Agassiz. Lower Old Red Sandstone. Restoration of shoulder-girdle in ventral view. After RSM 1887.35.5B, 1963.2.5; BM P.6964, P.1343a, 38596. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

The anterior lorical plate (*ALo*, 'median dermal bone', Watson 1937) has a ventral spine-bearing lamina (*vl*) and an ascending lamina (*al*) which rises for a short distance in the hind wall of the gill-chamber. Both laminae are arched, and they merge smoothly with each other so that the plate is hemicylindrical in cross-section. The plate shows no sign of subdivision into scales and it was not recognised as a structure distinct from the spine by Ørvig (1967). The last element may be termed the median prepectoral spine (*ppsp.m*; 'unpaired median prepectoral fin-fold spine', Ørvig 1967); it is open basally on the visceral surface of the plate (*cav.sp*, Text-fig. 26B). The posterior lorical plate (*PLo*; 'median ventral plate', Ørvig 1967) is probably the structure misinterpreted as a paired 'anterior admedian' by Watson (1937: 60; cf. Ørvig 1967 : 139). It is slightly too narrow in Ørvig's restoration, but is otherwise correctly placed. Unlike the anterior lorical it is overlain by scale-like plates. It is only necessary to add that the visceral surface exhibits an extensive, shallow pericardial depression (*dp.pc*).

The anterior pinnal plate (*APl*) was reasonably described as a 'cylindrical dermal bone' by Watson (1937 : 60), but was not distinguished from its spine by Ørvig (1967). Like the anterior lorical plate it has a ventral spine-bearing lamina (*vl*) and an ascending lamina (*al*). The margins are difficult to fix but it appears that the surface shows no subdivision into scale-like areas (Pl. 16, fig. 2). The spine is ventrally directed, and it may be termed paired prepectoral spine 1 (*ppsp1*; 'paired prepectoral fin-fold spine', Ørvig 1967); its cavity opens on the visceral surface of the plate.

The remaining pinnal plates are covered with scale-like elements. The middle pinnal (*M2Pl*, 'anterior lateral plate', Watson 1937; 'first ventrolateral plate', Ørvig 1967) again comprises ventral and ascending laminae, and at their junction arises a short, ventrolaterally directed spine. Because of the number of paired prepectoral spines in *Erriwacanthus falcatus* Ørvig (Text-fig. 27), this is here termed paired prepectoral spine 3 (*ppsp3*) and the plate is more correctly termed the second middle pinnal plate. Paired prepectoral spine 2 is held to be absent in *Climatius reticulatus*.[3] The cavity of the spine opens on the visceral surface in the angle between the two laminae. The posterior pinnal plate (*PPl*; 'second ventrolateral plate', Ørvig 1967) is more or less triangular and has no ascending lamina. Laterally it is firmly attached to the pectoral spine (*p.sp*), but whether in a butt joint or with an overlapping suture is not known (cf. *Diplacanthus*, p. 191). A short, ventrally-directed spine arises from its surface (*i.spl*; 'ridged dermal bone', Watson 1937; 'fin-fold spine of the ventro-lateral plate', Ørvig 1967). I now regard this, and its homologue in other climatiiforms, as the first intermediate spine. This differs from my earlier practice with diplacanthids (Miles 1966 : 169, footnote), although in this group Westoll (1958) has already included the spine ('admesial pectoral spine', Watson 1937) in counts of the intermediate series. As indicated above, the prepectoral, intermediate and pelvic spines form a continuous series. The pectoral spine lies lateral to this series (p. 206). The cavity of the first intermediate spine (*cav.sp*) opens on the visceral surface of its supporting dermal plate, exactly like the prepectoral spine. Thus I cannot agree with Ørvig (1967 : 137) that this spine differs from the prepectoral spines in its development. I agree with Ørvig, however, in concluding that Watson's paired 'posterior admedian' plates, between the posterior pinnals, have no real existence. The visceral surface of the posterior pinnal is raised into a low, broad ridge (*rdg.Pl*) around the mesial angle and anteromesial margin of the plate. There is some indication of a similar ridge around the posteromesial angle of the second middle pinnal plate.

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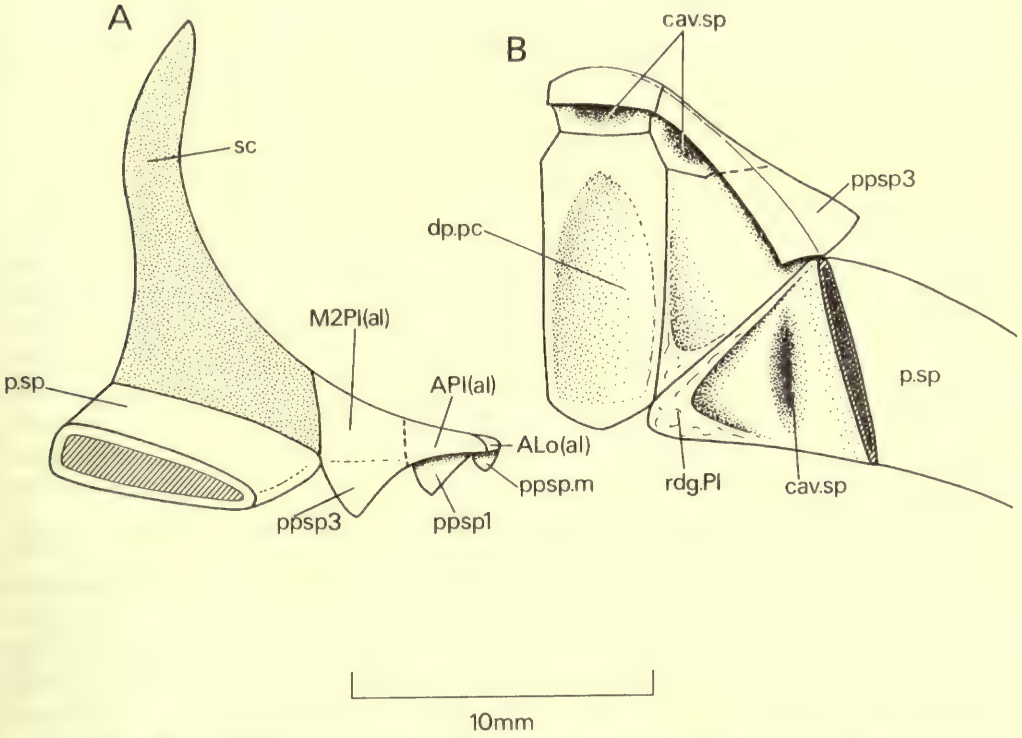
[3] It will be noted in the following accounts that there is some difficulty in determining the prepectoral spines in species in which their numbers have been reduced. The problems of homologising intermediate and prepectoral spines are discussed on p.197.

ENDOSKELETAL GIRDLE. The ossified endoskeleton (Text-fig. 26) is represented by the perichondral scapula (*sc*), which has been described by Watson (1937 : 60). Its lower lateral margin is firmly attached to the pectoral spine. Unfortunately, the exact extent of the anteroventral region cannot be determined, as here the perichondral bone becomes confused with the lateral laminae of pinnal plates, but it is likely that a coracoid process existed of comparable extent to that of *Ptomacanthus*



TEXT-FIG. 26. *Climatius reticulatus* Agassiz. Lower Old Red Sandstone. Restoration of shoulder-girdle in A, lateral view and B, dorsal view, with left lateral plates omitted. After RSM 1891.92.198, 1887.35.5A, 1963.2.5; BM P.1343, P.6964, P.6964a. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

(Text-fig. 4A) and other genera (Text-figs. 29, 31, 32). Although the coracoid region is unossified, it appears that it sat accurately over the posterior pinnal plate, and it had a broad posterior face which rose to a horizontal margo radialis in the middle region of the scapulocoracoid, mesial to the pectoral spine. The thickened rim of the second middle pinnal plate similarly received the mesial wall of the coracoid process, and the anteromesial ridge of the posterior pinnal received the base of an endochondral septum (p. 172).

A group of body scales is closely applied to the lower part of the lateral surface of the scapula (Pl. 2). This condition is, however, better seen in other genera (e.g. Text-fig. 29A).

PECTORAL FIN. The pectoral spine is shown in the illustrations, and there is no need to add to earlier descriptions. It is orientated with its proximal end above and its tip well below the base level of the ventral plates. The leading edge is carried slightly below the trailing edge, so that the spine is angled at about 10° to the horizontal.

The only other evidence of the pectoral fin is provided in a few specimens by patches of small scales in the appropriate region (Watson 1937, Pl. 5). These scales are less obviously arranged in rows than in other acanthodians, and are about 1/4 of the size of the adjacent flank scales. They nevertheless show that a well-developed pectoral fin with a sizeable web was present (cf. Westoll 1945 : 382).

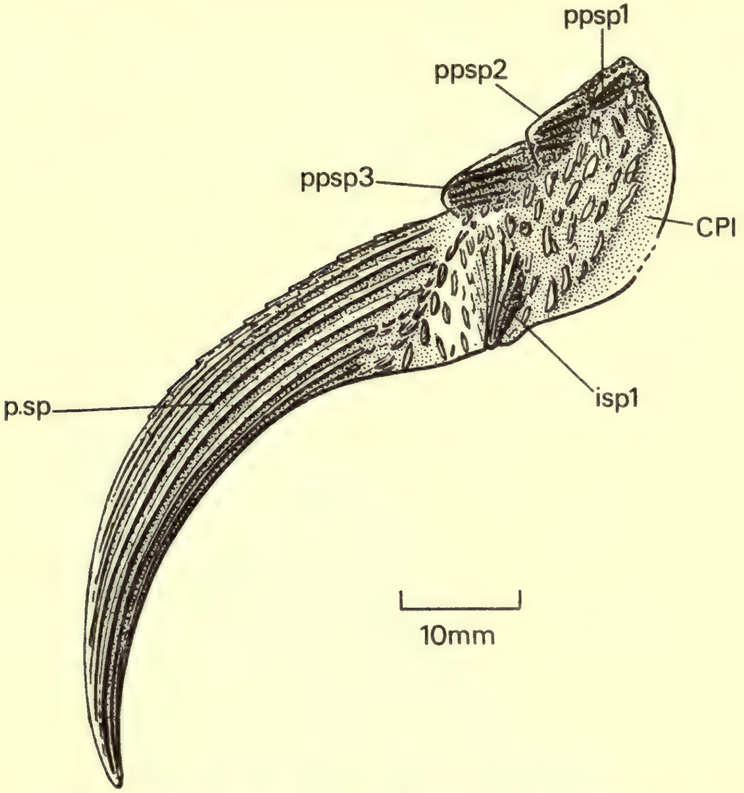
Erriwacanthus falcatus Ørvig

Ørvig (1967) has described under this head the right half of the dermal shoulder-girdle of a climatiid from the Old Red Sandstone of the Ukraine, which is preserved as an intaglio. The specimen (Text-fig. 27) comprises a long pectoral spine attached to an ornamented dermal plate (*CPl*; 'ventrolateral plate'). This plate is transversely arched in its posterolateral corner, so that the pectoral spine (*p.sp*) is carried above the base level. There are three flattened paired prepectoral spines (*ppsp1–3*) on its lateral margin before the pectoral spine, and the first intermediate spine (*isp1*) is attached mesially to the base of the pectoral spine. No sutures can be seen between the spines and the dermal plate, and there is no sign of the subdivision of the superficial layers of the plate into scale-like areas.

The plate may be termed the copinnal plate (*CPl*). It certainly includes the equivalents of the anterior, second middle and posterior pinnal plates of *Climatius reticulatus*. However, it follows from the hypothesis that these plates are each associated with one spine of the prepectoral-intermediate series, that there is an additional first middle pinnal plate component in *Erriwacanthus* associated with paired prepectoral spine 2. This spine (*ppsp2*) may also be present in *Vernicomacanthus* spp. and *Parexus* spp. (Text-figs. 14, 15A).

Whether or not the copinnal plate of *Erriwacanthus* was connected to its antimere by median plates (loricals) is unknown, but it seems probable that it was.

The endoskeletal shoulder-girdle and pectoral fin are unknown.



Text-fig. 27. *Erriwacanthus falcatus* Ørvig. Lower Old Red Sandstone. Right lateral region of shoulder-girdle in ventral view. After Ørvig 1967, Text-fig. 1A and cast BM P.29075. Upper part of Old Red, Dwinogrod, Ukranian SSR.

Erriwacanthus manbrookensis sp. nov.

Pl. 18, fig. 1

1967 *Parexus* sp.; Ørvig : 139, pl. 1, fig. 4

Etymology. From Man Brook.

Diagnosis. A species which differs from *E. falcatus* in the disposition of the three paired prepectoral spines, particularly in the wide spacing of prepectoral spines 2 and 3, and in the more lateral position of number 1.

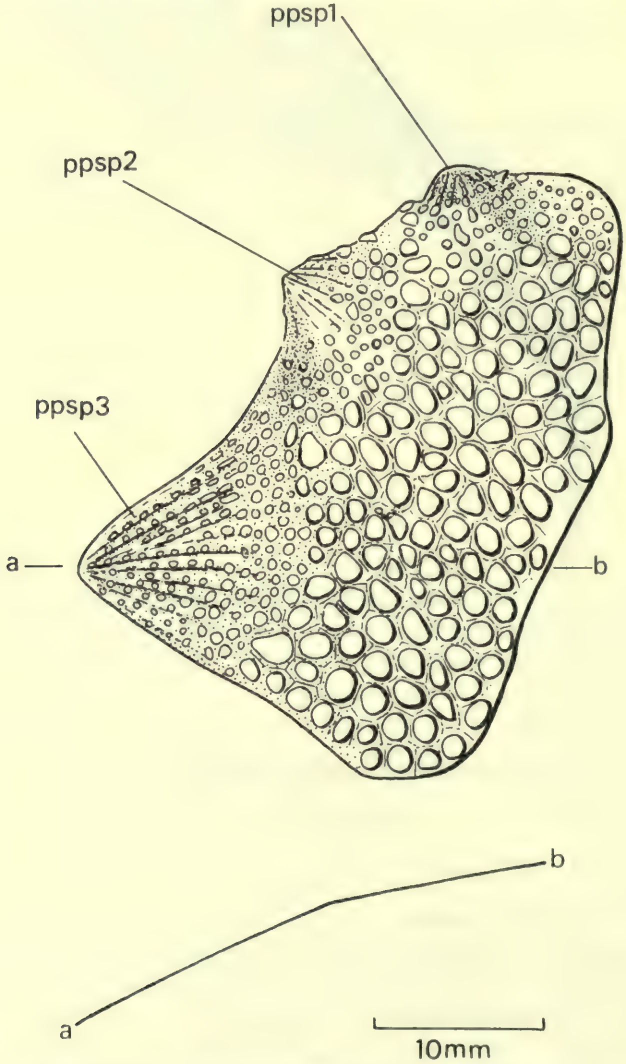
Type. The holotype is BM P.20185 (Ørvig 1967, Pl. 1, fig. 4).

Horizon. Downton Series, Red Marl Group, *Tesseraspis* zone (White 1950; 'stage I.6', King 1934).

Locality. Man Brook 7, Shatterford, near Trimpley, Worcestershire, England.

MATERIAL. BM P.20185, P.48984.

DESCRIPTION. Ørvig has figured two conjoined prepectoral spines (P.20185), but a second specimen (P.48984) shows that they are part of a series of three attached to an extensive ascending lamina of a compound pinnal plate (Text-fig. 28, Pl. 18, fig. 1). The ventral lamina of this plate and the endoskeletal girdle are still unknown. The ascending lamina is ornamented with large, smooth, low tubercles, which merge



TEXT-FIG. 28. *Erriwacanthus manbrookensis* sp. nov. Lower Old Red Sandstone. Ascending pinnal lamina and paired prepectoral spines in dorsolateral view, with profile a–b of superficial surface. After holotype, BM P.48984. Downton Series, Red Marl Group, Man Brook 7, Shatterford, Worcestershire, England.

almost abruptly with those situated on the ridges of the prepectoral spines. The ascending lamina shows no sign of subdivision into component pinnal plates. However, it is superficially subdivided into many small polygonal tesserae each with a single tubercle at its centre. The skeleton is thus comparable with the ventral plates of *Climatius reticulatus*, in the division of the superficial layer into scale-like areas which are attached to one or more large sheets of basal bone. The paired prepectoral spines are set at varying angles. Number 3 (*ppsp3*) projects ventrolaterally at some 15° away from the plane of the ascending lamina; number 2 (*ppsp2*) projects laterally in the plane of the lamina; and number 1 (*ppsp1*) also projects laterally, but is more prominently placed on the surface of the lamina than is number 2.

REMARKS. *Erriwacanthus manbrookensis* can be shown to resemble *E. falcatus* in only one character, the presence of three paired prepectoral spines. This may be the primitive number for climatioids (p. 196), and if so it is not good evidence that these species are congeners. However, there is neither evidence to relate *E. manbrookensis* to any other named genus, nor sufficient information to define or warrant the erection of a new genus. For these reasons the species is provisionally referred to *Erriwacanthus*. It differs from *Parexus* spp. in the presence of an extra paired prepectoral spine, presumably in the composition of the compound pinnal plate, and in its more extensive ascending lamina. Although the matter is not discussed by Ørvig (1967), it seems unlikely that these shoulder-girdle remains are conspecific with the spine described by Traquair (1894b, '*Parexus*') from the base of the Ditton Series (Cradley) in Herefordshire.

SABRINACANTHUS gen. nov.

ETYMOLOGY. L. *sabrina*, the River Severn; Gr. *akantha*, a thorn.

DIAGNOSIS. A climatiid with extensive, ornamented ventral and ascending pinnal laminae, which differs from *Erriwacanthus* and *Brachyacanthus* in the absence of paired prepectoral spine 1, and from *Climatius*, *Ptomacanthus* and *Brachyacanthus* in the presence of paired prepectoral spine 2; scapular blade with a slender dorsal shank.

TYPE SPECIES. *Onchus arcuatus* Agassiz 1837.

Sabrinacanthus arcuatus (Agassiz)

Pl. 17

1837 *Onchus arcuatus;* Agassiz : 7
1843 *Onchus arcuatus;* Agassiz, Pl. 1, figs 3–5
1844 *Byssacanthus arcuatus;* Agassiz : 111
1967 *'Onchus' arcuatus;* Ørvig : 140, text-fig. 3
1967 *Erriwacanthus* sp.; Ørvig : 135–136, Pl. 1, fig. 2

DEFINITION. The sole species referred to the genus.

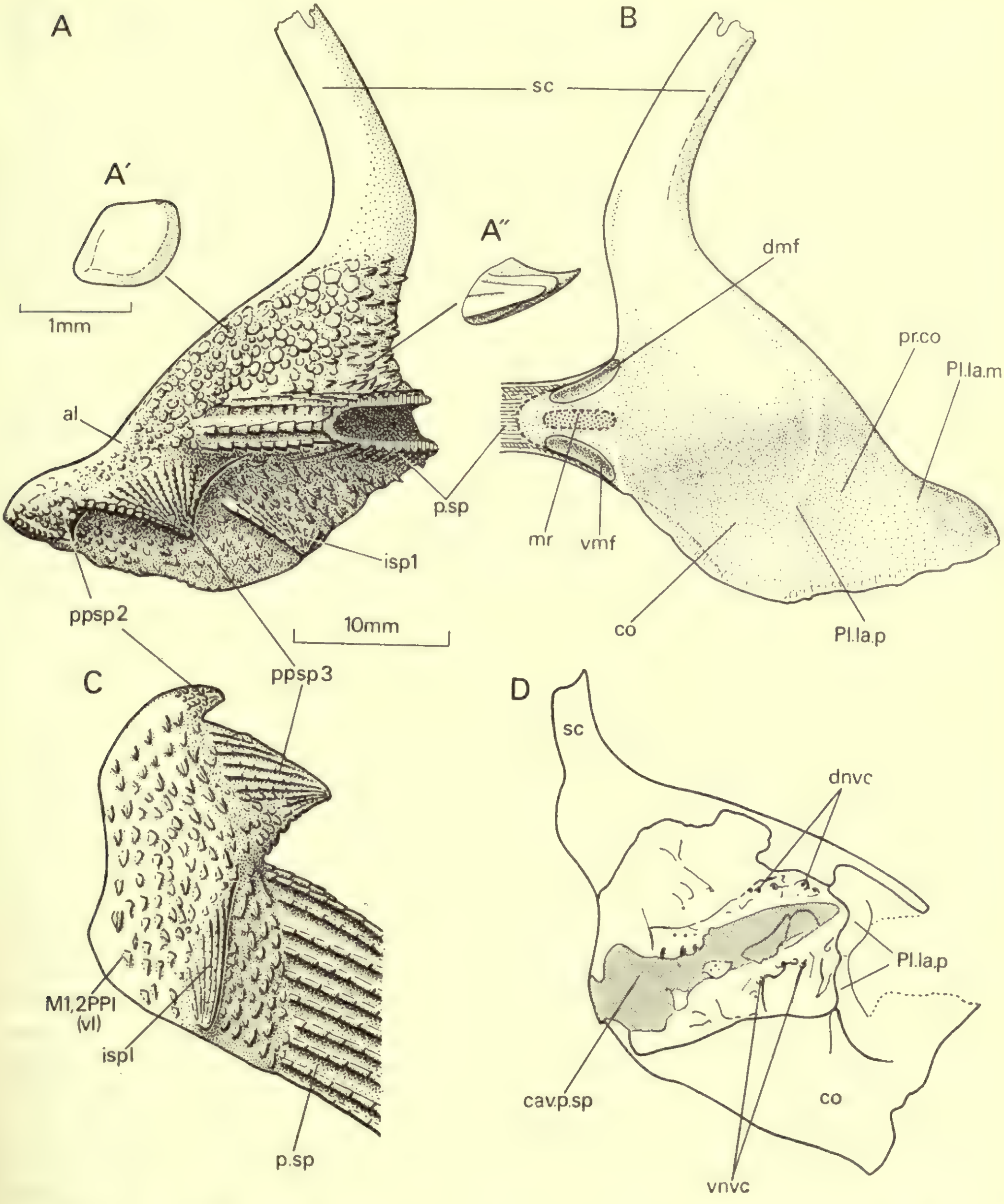
TYPE. Ørvig proposed that the specimen depicted by Agassiz in Pl. 1, fig. 4 (1843) should be the lectotype, but he did not point out that the whereabouts of this specimen are unknown. In fact the specimen may have been lost, together with others in the Murchison collection (Murchison 1853 : 16). A further complication is introduced by the possibility that the shoulder-girdle (UMO D17) figured by Ørvig (1967, Pl. 1, fig. 2) as *Erriwacanthus* sp. is the counterpart of this specimen. The locality of the former is given as Cradley, Herefordshire, and of the latter as Bromyard, but according to the best information now available these might well be the same locality (H. A. Toombs, pers. comm.). The ratios of pectoral spine curvature given by Ørvig for these specimens are remarkably alike, considering that one set is based on an illustration and the other on an incomplete specimen.

The present situation is clearly unsatisfactory, but in view of the possibility that a counterpart exists to the nominal lectotype, I propose to make no changes at this time.

HORIZON AND LOCALITIES. The following account is based on five specimens from the lower part of the Ditton Series, zone of *Pteraspis leathensis*. All are from the right bank of the R. Severn, Nass House, Lydney, Gloucester, England.

MATERIAL. The specimens are as follows: BM P.53120a, b; P.53121a, b; P.53122a, b; P.53123a, b; P.53124a, b. All show articulated parts of the shoulder-girdle. The first specimen has been positively prepared, and the last four have been negatively prepared with diluted hydrochloric acid and studied with the aid of rubber casts (Pl. 17).

DERMAL SKELETON. It is probable that median ventral dermal elements existed, comparable with the loricals of *Climatius reticulatus*, but they have not been preserved. This account is concerned, therefore, with paired lateral plates and their spines. There is a compound pinnal plate (*M1,2PPl*) with a prominent ornamentation on its ventral (*vl*) and ascending (*al*) laminae (Text-fig. 29, Pl. 17, figs. 2, 3). Laterally it gives rise to a pectoral (*p.sp*) and two paired prepectoral spines (*ppsp2, ppsp3*). Mesial to the pectoral spine, which is inserted well above the base level of the girdle, the ventral lamina carries a prominent first intermediate spine (*isp1*). All of the spines are ornamented with characteristically-noded, climatiid ribs, and are basally open. The pinnal ornament shows pronounced regional variation. On the ascending lamina it comprises low, broad tubercles (Text-fig. 29A, A′, Pl. 17, fig. 3), and this ornamentation is carried back on to the anterior part of the base of the scapula by modified body scales which are closely applied to its surface. It is impossible to draw a firm boundary between the ascending lamina and this field of scales. The whole region lay in the postbranchial wall and in ornamentation recalls the ascending lamina of *Erriwacanthus manbrookensis*. On the ventral lamina the ornamentation comprises high, ribbed tubercles, similar to those found in *Erriwacanthus falcatus* (Ørvig 1967, Pl. 1, fig. 1). A comparable ornamentation is produced on the posterolateral face of the base of the scapula by a field of closely applied high-crowned, body scales (Text-fig. 29A, A″, C). The visceral surfaces of the pinnal laminae are overlain by the scapulocoracoid, and cannot be observed.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C
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Pl.la.p
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TEXT-FIG. 29. *Sabrinacanthus* gen. nov. *arcuatus* (Agassiz). Lower Old Red Sandstone. A, B, C, restorations of the shoulder-girdle in lateral, mesial and ventral views, with A′, A″ enlarged drawings of the dermal ornamentation. After BM P.53120 and P.53122. D, key-diagram for Pl. 17, fig. 1, showing internal structure in region of the pectoral spine. BM P.53122. Ditton Series, Nass House, Lydney, Gloucestershire, England.

The posterior of the two paired prepectoral spines is situated immediately anteroventral to the pectoral spine, and is laterally directed. Without question it is the topographic homologue of spine number 3 in *Climatius* and *Erriwacanthus*. The anterior spine is carried immediately anteroventral to the posterior, and is also laterally directed. For these reasons it is determined as paired prepectoral spine 2. The alternative determination as spine number 1 is rejected, because unlike the first spine in *Climatius* it is not ventrally directed, and it is not separated from spine number 3 by a distinct gap. It follows from the determinations of these spines and the inclusion of the first intermediate spine in the girdle, that the dermal skeleton comprises first and second middle pinnal plate and posterior pinnal plate components. There is no external sign of the division of the skeleton into its components by sutures, and no evidence of an anterior pinnal plate component.

Endoskeletal girdle. This is unusually well preserved and comprises perichondrally ossified scapular (*sc*), coracoid (*co*) and coracoid process (*pr.co*) regions (Text-fig. 29B). These regions merge smoothly with each other in the middle region, and therefore do not have sharply defined proximal boundaries. Dorsally the scapula forms a high, narrow, oval shank, which is quite distinct from the broad scapular blade of *Ptomacanthus* but is comparable with *Climatius*. Ventrally this region is anteroposteriorly expanded, and from here the mesial wall of the scapulocoracoid sweeps down over the ventral pinnal lamina in a hollow curve. The coracoid process is contained within the ventral and ascending laminae of the anterior half of the pinnal plate. The cavity of the lower region of the scapulocoracoid (originally solid cartilage) is partitioned by two stout endoskeletal laminae, which are discernible in the undissected girdle as slight ridges on the surface of the perichondral bone. The posterior lamina (*Pl.la.p*) lies in the plane of the junction between the pectoral and first intermediate spines. It is now possible to interpret the visceral ridge which runs along the anteromesial margins of the posterior pinnal plate in *Climatius reticulatus*. It may have supported the base of an exactly comparable endochondral lamina, whilst other parts of the ridge supported the mesial perichondral wall of the coracoid and coracoid process (*rdg.Pl*, Text-fig. 26B). The anterior partition in *Sabrinacanthus* (*Pl.la.m*) lies between the planes of paired prepectoral spines 2 and 3, and thus divides the regions of the scapulocoracoid associated with the first and second middle pinnal plates. There is neither evidence of a homologous lamina in *Climatius reticulatus* (paired prepectoral spine 2 is absent), nor of a partition at the posterior margin of the anterior pinnal plates. Thus in *Sabrinacanthus* there is evidence of the division of the girdle into its component pinnal regions, despite the absence of any indication of this in the dermal skeleton.

Laterally, the middle region of the scapulocoracoid extended in life into the cavity of the pectoral spine. In two specimens (P.53120a, b; P.53123a, b) the base of the resulting lateral process is partly perichondrally ossified on its posterior surface, and thus provides some information on the fin articulation area. At the base of the spine, facing posteriorly, there are horizontal dorsal and ventral muscle attachment surfaces (*dmf*, *vmf*, Text-fig. 29B). Each is in the form of a shallow trough.

Between them, in an unossified area, there must have been a short, horizontal margo radialis (*mr*). The position and small size of the muscle attachment areas, taken with the immobility of the pectoral spine, suggests that the fin muscles were smaller and less differentiated than those of *Acanthodes*.

During the negative preparation of P.53122a, b the inner face of the lateral wall of the scapulocoracoid was observed, in the region of the pectoral spine (Pl. 17, fig. 1, use Text-fig. 29D as key drawing). Both above and below the opening of the cavity of the pectoral spine (*cav.p.sp*), the perichondral bone is irregularly grooved and perforated by fine foramina (*dnvs*, *vnvs*). I interpret these features as evidence for dorsal and ventral neurovascular systems. Their relationship to the scapulocoracoid and pectoral fin is similar to that of the cutaneous nerves and vessels which penetrated the shoulder-girdle in a number of placoderms (Stensiö 1944, 1959).

There are no major foramina in the walls of the scapulocoracoid which might be compared with the coracoid foramen and subscapular fossa of *Acanthodes*. The fin of *Sabrinacanthus* must, therefore, have been innervated solely by metazonal nerves.

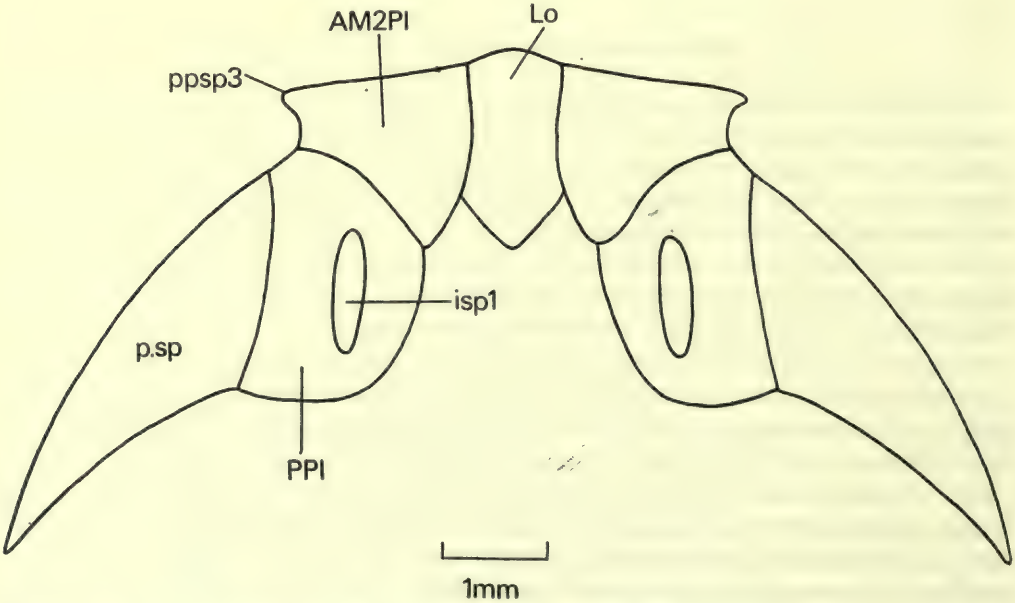
PECTORAL FIN. This structure is represented only by the curved, ribbed pectoral spine. It is seen in Pl. 17, fig. 2 (also Ørvig 1967, Text-fig. 3, Pl. 1, fig. 2), and requires no additional description. In orientation it corresponds closely with the spine of *Climatius reticulatus* (p. 166).

Brachyacanthus scutiger Egerton

This is the smallest and least well preserved of the Scottish Lower Old Red Sandstone climatiiforms, and its shoulder-girdle cannot be worked out in the same detail, or with the same degree of confidence, as in other species. I have recently classified *Brachyacanthus* with the Climatiidae (Miles 1970 : 362), although prior to this it was placed in the Euthacanthidae (Berg 1958; Miles 1966). This move is supported by the structure of the shoulder-girdle, although it was first suggested by the dermal skeleton of the head (Watson 1937, Text-fig. 5) and the apparent presence of small teeth in GSE 10408 from Duntrune Quarry, Angus.

DERMAL SKELETON. The following tentative interpretation (Text-fig. 30) is suggested by BM 35908 and P.6957, both from Farnell, Angus. The short pectoral spine (*p.sp*) is attached to a well-developed posterior pinnal plate (*PPl*; ? 'enlarged scale', Watson 1937 : 70), which bears the basally-open first intermediate spine (*isp1*). Anteromesially the posterior pinnal abuts against the ventral lamina of a further paired plate which carries a laterally-directed prepectoral spine. This plate is probably the 'anterolateral dermal bone' of Watson (1937, Text-fig. 5); mesially it is connected to a median lorical plate. The 'antero-lateral' is not easy to homologise with the plates of *Climatius reticulatus*, but because it is in contact with both the posterior pinnal and a lorical plate, it may be regarded as an anterior-middle pinnal plate (*AM2Pl*). Its spine, which is not separated from the plate by a distinct suture, may be tentatively determined as paired prepectoral spine 3 (*ppsp3*), although until the composition of the plate is known in detail it might equally well be regarded as paired prepectoral spine 2. Like the first intermediate spine, it has a distinctive ornamentation of ridges, similar to those of the pectoral spine. The median plate is too extensive to be readily accepted as the topographic homologue of the anterior lorical, and it may equal both the anterior and posterior loricals of *Climatius*. No transverse suture can be seen dividing the plate, but such is the preservation that one could well have existed. The plate is provisionally termed the lorical (*Lo*). I have not observed a median prepectoral spine, but again one might well have existed and not be discernible in the specimens at hand. The three plates just described appear to be ornamented bones not covered by scales, and they are not subdivided into scale-like areas.

Endoskeletal girdle. The scapulocoracoid is ossified as a scapula, which has been accurately figured and described by Watson (1937 : 69, Text-fig. 5). This structure is closely comparable with the scapulae of other climatiids, and it would be superfluous to redescribe it. The only new information is provided by BM P.6984 from Denoon, Angus, in which the lateral surface of the scapula is ornamented in its lower regions with fine, well-spaced tubercles. A prolonged examination suggests that this is because a group of body scales of normal size has become firmly united to the scapula.



Text-fig. 30. *Brachyacanthus scutiger* Egerton. Lower Old Red Sandstone. Plan of ventral surface of shoulder-girdle. After BM P.6957, 35908. Arbuthnott Group, Dundee Formation, Farnell, Angus, Scotland.

Pectoral fin. Only the spine is known. It is shown in outline in Text-fig. 30, and has been described in some detail by Watson (1937 : 69).

Ptomacanthus anglicus

It is desirable to give a brief summary of the shoulder-girdle in this species, in the light of the more primitive dermal structures described above in other climatiids.

Dermal skeleton. The pinnal plate(s) probably comprises a deeply-seated sheet of thin bone with ventral and ascending laminae (p. 164). Its detailed composition is not clear, but the paired prepectoral spines have a position comparable with those of *Climatius* and may be determined as numbers 1 and 3 (*ppsp1*, *ppsp3*, Text-fig. 4). The first intermediate spine may or may not have been attached to the girdle (p. 122), but it appears that the pinnal plate extends posteriorly below the coracoid region, mesial to the pectoral spine. Thus the pinnal plate is provisionally regarded as including anterior, second middle (p. 164) and posterior components (*AM2PPl*). It is covered by scales, which may represent the superficial layer of the dermal skeleton, as in *Climatius* and *Erriwacanthus manbrookensis*, but may alternatively, because of their form, represent a secondary extension of the trunk squamation over the girdle. The scales have broad, flat crowns on the ascending lamina, as in *Sabrinacanthus*. There is a median prepectoral spine (*ppsp.m*) and, therefore, probably an anterior lorical plate. There is no evidence of a posterior lorical plate.

Endoskeletal girdle. This is notable for the high, broad scapula (*sc*), deep coracoid (*co*) and well formed coracoid process (*pr.co*, Text-fig. 4).

Ptomacanthus sp. indet 1

I shall describe here two shoulder-girdles from the Old Red Sandstone of England which show well some of the detail of the scapulocoracoid. Both specimens closely recall *Ptomacanthus anglicus*, but they are from a different stratigraphical horizon and appear to differ in some details of form from this species. Empiric evidence suggests that individual species of fishes have a short vertical range and limited lateral distribution in the *Pteraspis crouchi* zone of the English Old Red Sandstone (White 1950 : 58, footnote). For these reasons the specimens are not given a trivial name. They seem clearly to be conspecific with each other.

Material and localities. BM P.17290–1, the right half of a shoulder-girdle in part and counterpart, slightly incomplete and negatively prepared, from Castle Mattock quarry, Cladock, SW. Herefordshire. BM P.23789, the right half of a shoulder-girdle seen in lateral view, from Wern Genni quarry, SW. Herefordshire.

Horizon. Ditton Series. Castle Mattock quarry is about 73 m and Wern Genni quarry about 198 m above the main '*Psammosteus*' Limestone (White 1950 : 58, footnote); in the *Pteraspis crouchi* zone.

DESCRIPTION. The restorations (Text-figs 31, 32) are based mainly on P.17290–1 (Pl. 19, fig. 1) and show the salient features of the scapulocoracoid and pectoral spine. The spine (*p.sp*) is broad, gently curved and somewhat triangular in cross-section. It is ornamented with prominent ridges which become slightly beaded proximally. These ridges are, however, missing most proximally where the spine was inserted in the body wall and attached to the girdle. The cavity of the spine opens proximally on its mesial face (*cav.p.sp*), but was presumably filled with an extension of the girdle in life, as in *Sabrinacanthus*.

The scapulocoracoid is invested by a thin coat of perichondral bone. The scapular blade (*sc*) is broad and thin (see section, Text-fig. 31). It is incomplete dorsally in both specimens. The mesial face of the middle region lacks perichondral bone, adjacent to the opening of the pectoral spine cavity (*cart* (*mr*), Text-fig. 32). This region of the girdle probably included the margo radialis and muscle attachment areas, as in *Sabrinacanthus*. The coracoid region (*co*, Text-fig. 31B) merges smoothly with the more dorsal parts of the girdle. The long coracoid process (*pr.co*) is more or less triangular in section proximally (posterolaterally), with ventromesial, dorsomesial and lateral faces, but distally it tapers and becomes almost oval in section. The dorsomesial face is hollowed, except most laterally, and it may have provided a surface for the origin of hypobranchial muscles. The ventromesial face is featureless. The lateral face cannot be seen in P.17290–1, either because it was not ossified or more probably because it has not been successfully exposed by negative preparation. P.23789 has been partly prepared to show this wall, and although the specimen is not entirely satisfactory, it seems clearly to demonstrate the absence (post-mortem) of prepectoral spines. What is not clear is whether any thin dermal bone remains on the lateral and ventral surfaces of the coracoid and coracoid process.

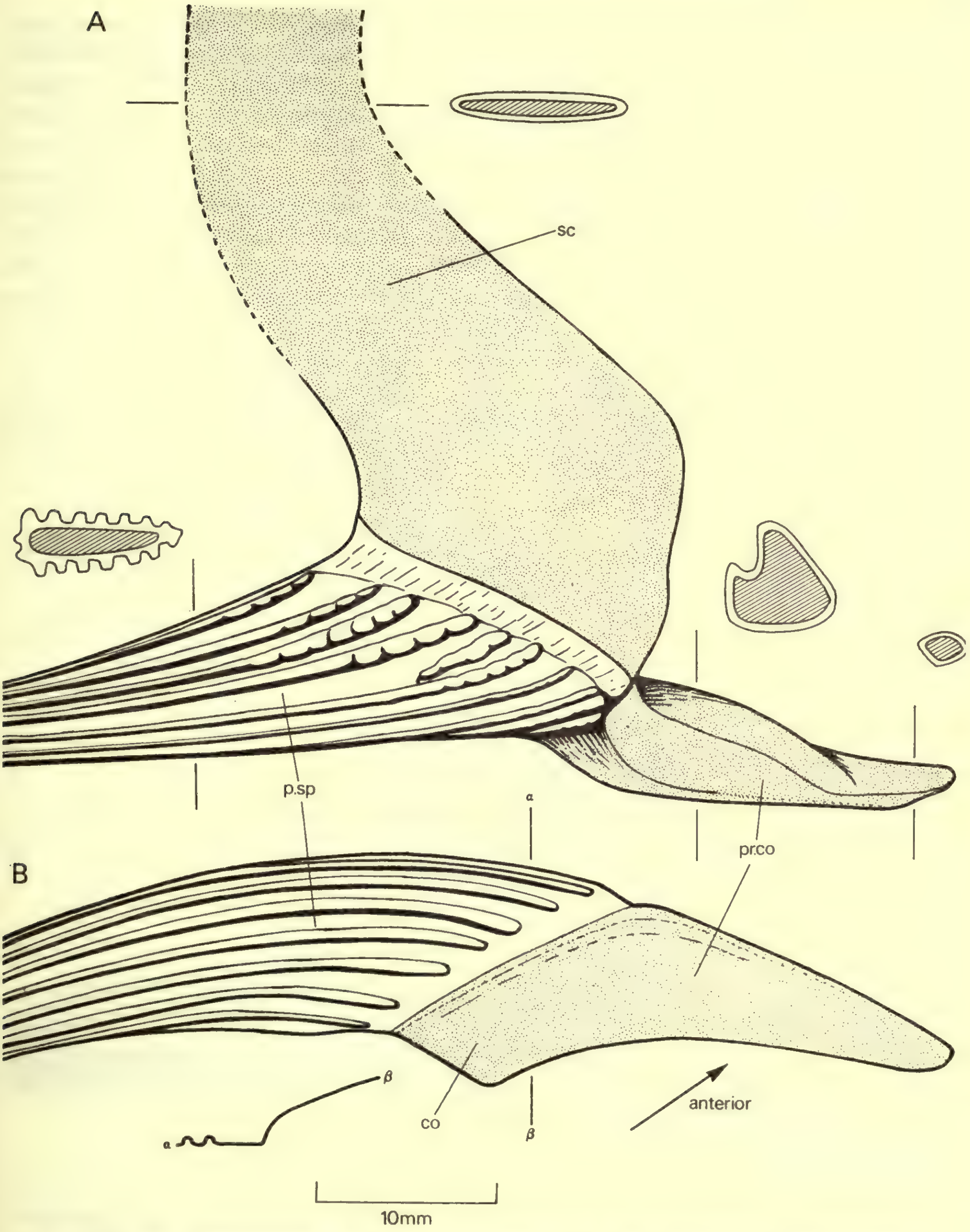
The tips of the left and right coracoid processes probably touched in the middle line, and they may have been firmly united by ligaments.

Ptomacanthus sp. indet 2

Although it adds little to our knowledge in connexion with the present paper, it is interesting to record the existence of a shoulder-girdle of *Ptomacanthus* sp. (SMNH P.6841; cast BM P.53040) from the Dittonian of Zaleszychi, Ukranian SSR, which closely resembles *Ptomacanthus* sp. indet 1. This specimen (Pl. 20, fig. 1) confirms the high tapering form of the scapular blade.

Vernicomacanthus uncinatus (Powrie)

All the remaining species of Devonian climatioids to be described are alike in the complete reduction of the ventral laminae of the pinnal plates, and therefore in the suppression of the posterior pinnal and in the separation of the pectoral and first intermediate spines from the dermal plates. The pinnal plates are represented

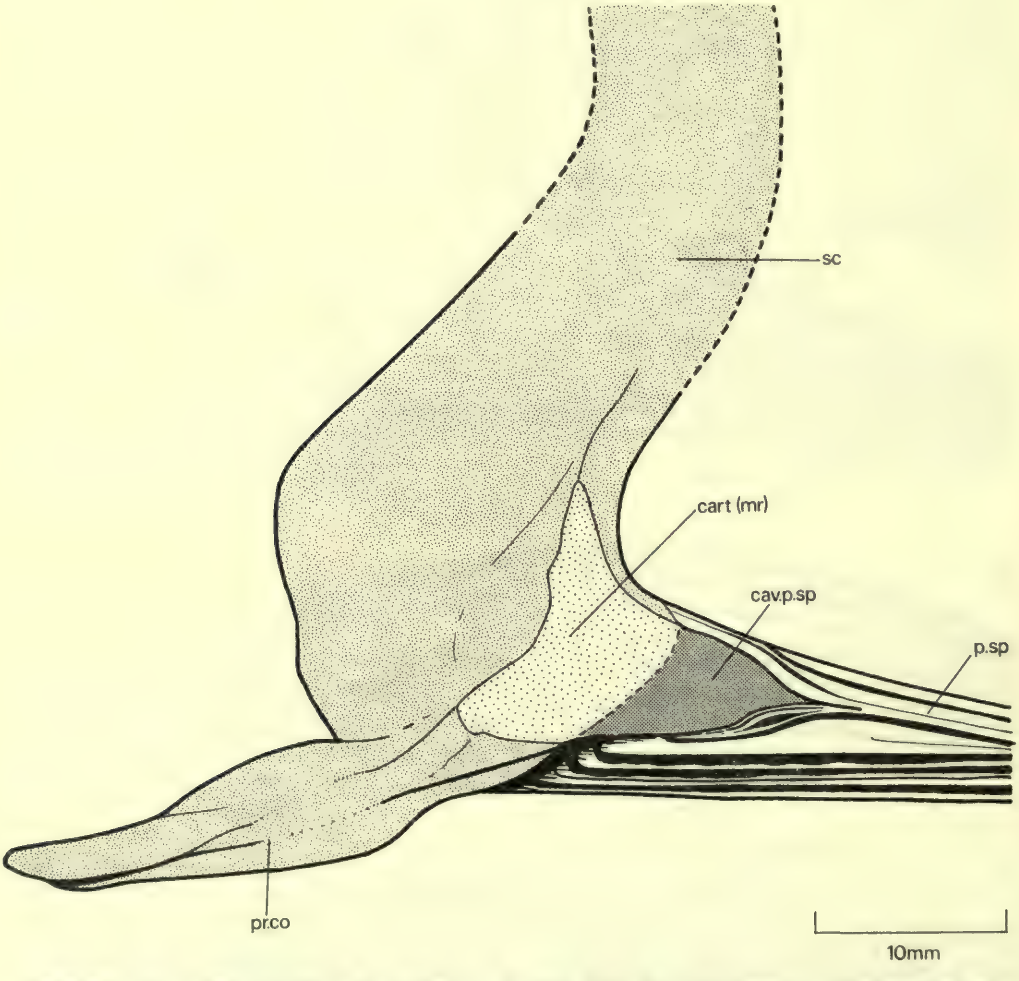

A
sc
p.sp
α
pr.co
B
co
β
α
β
anterior
10mm

TEXT-FIG. 31. *Ptomacanthus* sp. indet. 1. Lower Old Red Sandstone. Restoration of shoulder-girdle in A, lateral and B, ventral view with sections and profile A–B as indicated. After BM P.17290–1. Ditton Series, Castle Mattock quarry, Cladock, Herefordshire, England.

solely by their ascending laminae and accompanying paired prepectoral spines. These laminae were situated in the hind wall of the branchial chamber, immediately in front of the scapulocoracoid. The posterior lorical has also been suppressed in all of these species, although the anterior lorical is retained in some and may have both ventral and ascending laminae.

The above statements are based on the assumption that *Climatius reticulatus* is a more primitive species than those which follow. This assumption is explained below (p. 195).

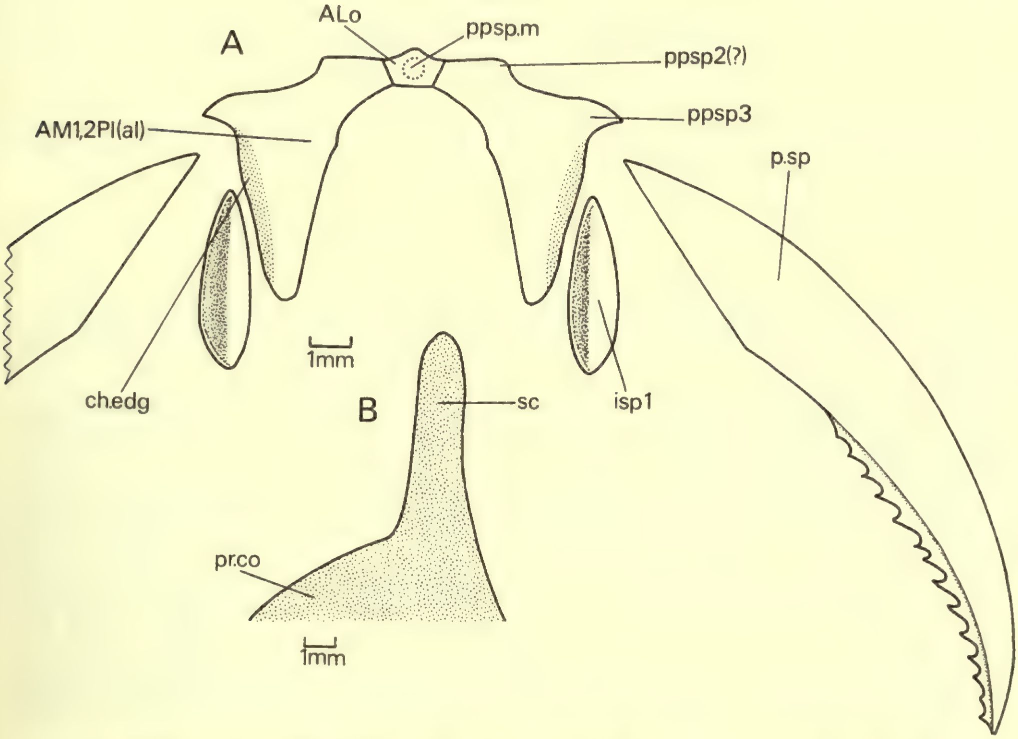
Climatius uncinatus Powrie has been referred to the new genus *Vernicomacanthus* on p. 140.



TEXT-FIG. 32. *Ptomacanthus* sp. indet 1. Lower Old Red Sandstone. Restoration of shoulder-girdle in mesial view. After BM P.17290–1. Ditton Series, Castle Mattock quarry, Cladock, Herefordshire, England.

Dermal skeleton. There is an anterior lorical (*ALo*) and a compound ascending lamina which represents the anterior and one or two middle pinnal plates (*AMPl*, Text-fig. 33, Pl. 7). The anterior lorical is arched and ends in a distinct dorsal angle, but the ventral and ascending laminae do not quite form a hemicylinder. Ventrally the plate carries a short median prepectoral spine (*ppsp.m*) which has a large central cavity.

The ascending pinnal lamina sutures with the ascending lamina of the anterior lorical plate. Laterally the pinnal lamina bears a short, basally open spine, which may be regarded as paired prepectoral spine 3 (*ppsp3*) by comparison with other genera. Further forwards the lamina is expanded into a lateral elbow, three mm or so to the side of the anterior lorical plate. I provisionally accept this as the site of a small prepectoral spine, which is too badly preserved to be observed clearly. By comparison with *V. waynensis* (p. 180, Text-figs. 14, 15A) it is determined as paired prepectoral spine 2. As the ascending lamina sutures with the anterior lorical plate, it is assumed to include an anterior pinnal plate component. Thus the



Text-fig. 33. *Vernicomacanthus* gen. nov. *uncinatus* (Powrie). Lower Old Red Sandstone. A, plan of shoulder-girdle in dorsal view, position of median prepectoral spine on ventral surface shown with dotted line. B, lateral view of scapulocoracoid. After RSM Kinnaird collection 82, 1891.92.210, BM P.1342a. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

ascending lamina comprises components of the anterior, and first and second middle pinnal plates (*AM1,2Pl*). The posterior margin of the pinnal lamina is bevelled (*ch.edg*), where the plate emerges laterally from the postbranchial wall.

The lorical and pinnal dermal plates show no sign of subdivision into scale-like areas and are ornamented with irregularly arranged, flat-topped tubercles which are transformed into three or four ill-defined ridges on paired prepectoral spine 3. The median prepectoral spine bears a few small tubercles. The pectoral spines have the normal climatioid ribbed ornamentation, but unlike other Scottish Lower Old Red Sandstone species, the ridges are obliquely placed as in *Gyracanthus incurvus* Traquair from the Lower Devonian of Canada (Woodward 1892a, Pl. 1, fig. 4). There is also a series of prominent denticles on the trailing edge of the spine. The first intermediate spine is situated mesially to the base of the pectoral spine. These two spines and the anterior lorical plate are separated from each other by regular rows of body scales (Pl. 7).

ENDOSKELETAL GIRDLE. The scapula is perichondrally ossified, with a coracoid process, and it has a similar relationship to the pectoral spine and dermal girdle as in other climatioids. The figure (Text-fig. 33B) requires no further comment.

PECTORAL FIN. The endoskeleton and dermotrichia of the fin are unknown, but minute scales from the ventral surface of the web are preserved in BM P.6960 and RSM 1891.92.210. These scales appear to lie in rows across the web rather than in proximo-distal rows, but this may be an artifact of preservation. The shape and size of the web are unknown, although clearly it was well developed.

Vernicomacanthus waynensis

This species has been described in the first part of this paper (p. 140). The composition of the dermal shoulder-girdle may be summarised here in the light of the results gained so far.

There are two paired prepectoral spines carried by an undivided ascending pinnal lamina. The posterior spine (*ppsp3*, Text-figs. 14, 15A) is situated immediately anteroventral to the pectoral spine, and by comparison with forms such as *Erriwacanthus*, *Climatius* and *Sabrinacanthus*, it can be confidently determined as paired prepectoral spine 3. The anterior spine (*ppsp2*) lies immediately in front of spine number 3. I have determined it as paired prepectoral spine 2, as indicated above in the description of *V. uncinatus*, because of its position and because it is ventrolaterally directed. Paired prepectoral spine 1 is more ventrally directed and more ventromesially situated than this in *Erriwacanthus falcatus* and *Climatius reticulatus*, and I have, therefore, rejected paired prepectoral spine 1 as an alternative determination.

The anterior lorical is reduced to a large tessera without an ascending lamina, and there is no median prepectoral spine (*ALo*, Text-fig. 14). The anterior lorical has no contact with the ascending pinnal lamina. Ventrally the various spines and the anterior lorical are separated from each other by an irregular field of large scales.

The separation of the anterior lorical plate and ascending pinnal lamina raises the question of the composition of this last structure, specifically whether it includes an anterior pinnal plate component. There is no means of answering this question, but provisionally I shall assume that this component is present, as in *V. uncinatus.* The ascending lamina (*AM1,2Pl*) is then believed to include anterior, and first and second middle pinnal components, as in *V. uncinatus. V. waynensis* is more advanced than *V. uncinatus* in the reduction of the anterior lorical and in the separation of this plate from the pinnal lamina; it is possibly more primitive in the greater size of paired prepectoral spine 2.

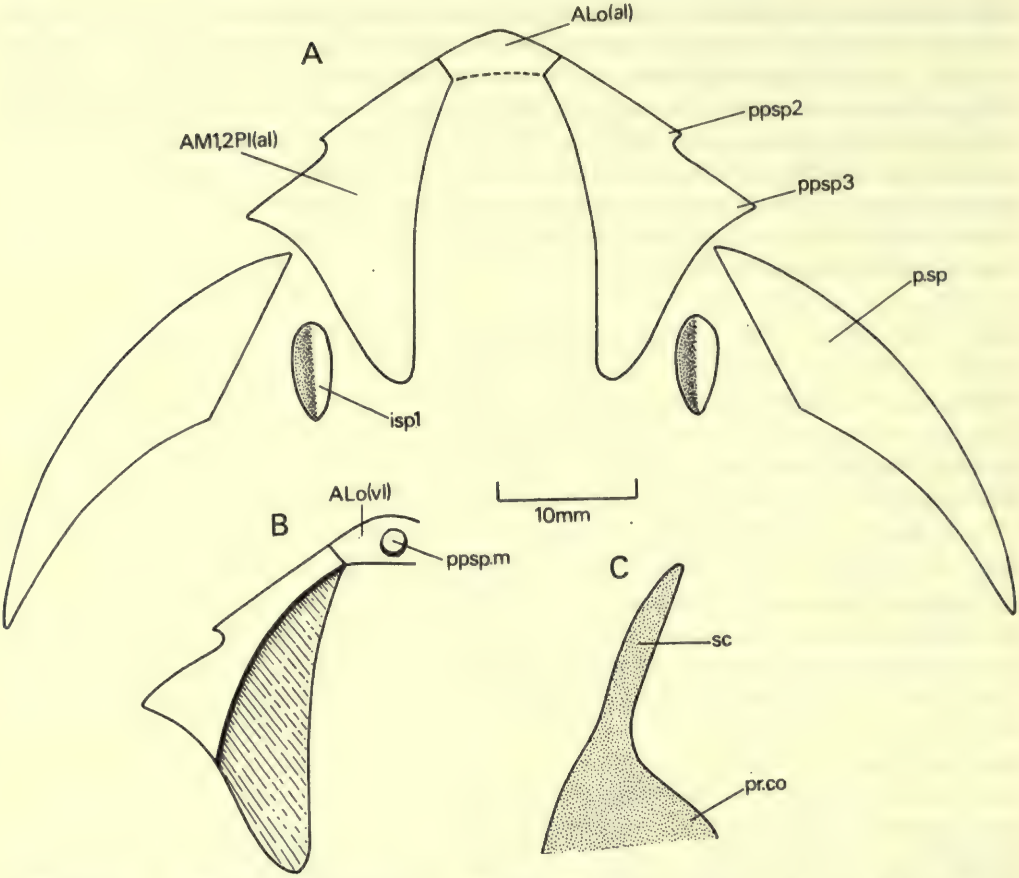
Parexus falcatus Powrie

It is convenient to describe this species before the type, *Parexus recurvus* Agassiz, because two specimens show the dermal plates of the shoulder-girdle flattened but in their natural relationship to each other. These specimens are from the Lower Old Red Sandstone of Turin Hill, Scotland, and bear the numbers RSM 1891.92.207 (Pl. 16, fig. 1) and BM P.130 (in counterpart) (Woodward 1891, Text-fig. 4; Dean 1907, Text-fig. 21). Both specimens show the lateral plates in visceral view.

DERMAL SKELETON. The ornamented dermal plates (Text-fig. 34) show no sign of subdivision into scale-like areas. They comprise the median anterior lorical (*ALo*), and a paired ascending pinnal lamina (*AMPl*, 'clavicle', Woodward 1891). The anterior lorical has a hemicylindrical section with ventral and ascending laminae which merge smoothly with each other. The ventral lamina bears a short, basally-open, median prepectoral spine (*ppsp.m*). The ascending pinnal lamina gives rise to two short, laterally-directed spines with basally-open cavities. The posterior of these spines is paired prepectoral spine 3 (*ppsp3*). The anterior may be determined as paired prepectoral spine 2 (*ppsp2*), with exactly the same arguments I have used in the case of *Vernicomacanthus waynensis.* The pinnal lamina thus comprises anterior, and first and second middle pinnal plate components (*AM1,2Pl*). As in *Vernicomacanthus* the pectoral spine (*p.sp*) and the first intermediate spine (*isp1*) stand free of the dermal shoulder-girdle. In both genera these spines retain the same spatial relationships to the surviving plates that they have in species such as *Climatius reticulatus.* Scale fields comprising slightly enlarged body scales separate the lorical plate and detached spines on the ventral surface. The scales tend to form antero-posterior rows between the paired prepectoral spines, but more posteriorly they merge with the normal body scaling.

ENDOSKELETAL GIRDLE. The preserved endoskeleton is the perichondrally ossified scapula (*sc*), which has a high cylindrical shank and a broad ventral plate which is attached to the upper edge of the pectoral spine.

PECTORAL FIN. The endoskeleton and dermotrichia are unknown, but both specimens show the fin web in the form of numerous small scales. Unfortunately these are poorly preserved, but they show that the web extended beyond the pectoral spine for a distance at least equal to half the length of the spine.



TEXT-FIG. 34. *Parexus falcatus* Powrie. Lower Old Red Sandstone. A, plan of shoulder-girdle in dorsal view. B, plan in ventral view, with right plates omitted; C, lateral view of scapulocoracoid. After RSM 1891.92.207, 1887.35.4, BM P.130. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

Parexus recurvus Agassiz

Since Powrie (1864, 1870), there has been a tendency to refer to this species in the incorrect form *Parexus incurvus* (Woodward 1891; Watson 1937; Westoll 1945; Ørvig 1967). The correct form will, however, be found in Traquair (1894a, b) and Waterston (1954). *Parexus recurvus* occurs in the Lower Old Red Sandstone of Turin Hill, and it is said to differ from *P. falcatus* in its smaller size, relatively smaller head and relatively longer, straighter first dorsal fin-spine. Whether this species separation is justified is perhaps open to question, as some of these differences can be accounted for by the normal processes of growth. With respect to the shoulder-girdle there appear to be no important differences of structure. The following notes, therefore, are given to supplement the account of *P. falcatus*. They are based on RSM 1956.14.14, 1887.35.3A, 1891.92.190 and 1891.92.188.

DERMAL SKELETON. The ascending pinnal lamina has been mistaken for a ventral plate by Watson and Ørvig ('antero-lateral dermal bone', Watson 1937; 'ventrolateral plate', Ørvig 1967). It is ornamented with irregular rows of flat, leaf-like tubercles, which become smaller and more regularly arranged on the paired prepectoral spines (Pl. 19, fig. 2; Ørvig 1967, Pl. 1, fig. 31). The posterolateral margin of this lamina is bevelled almost to the tip of paired prepectoral spine 3, as in *Vernicomacanthus uncinatus* (p. 180). The anterior lorical plate is also ornamented with flat tubercles, but these are arranged in tightly-packed rows which run mostly in the antero-posterior direction, although they converge on the spine. Both the median and the paired prepectoral spines are basally open.

ENDOSKELETAL GIRDLE. The scapular ossification is exactly comparable with that of *Parexus falcatus*. RSM 1891.92.188 and 1891.92.190 are of particular interest because they have enlarged body scales closely applied to the lateral surface of the shoulder-girdle (Text-fig. 35). These scales are about twice as big as the adjacent flank scales and are arranged in irregular antero-posterior rows. A similar patch of scales is less well seen in *P. falcatus* (BM P.130; Dean 1907 : 217, Text-fig. 27).

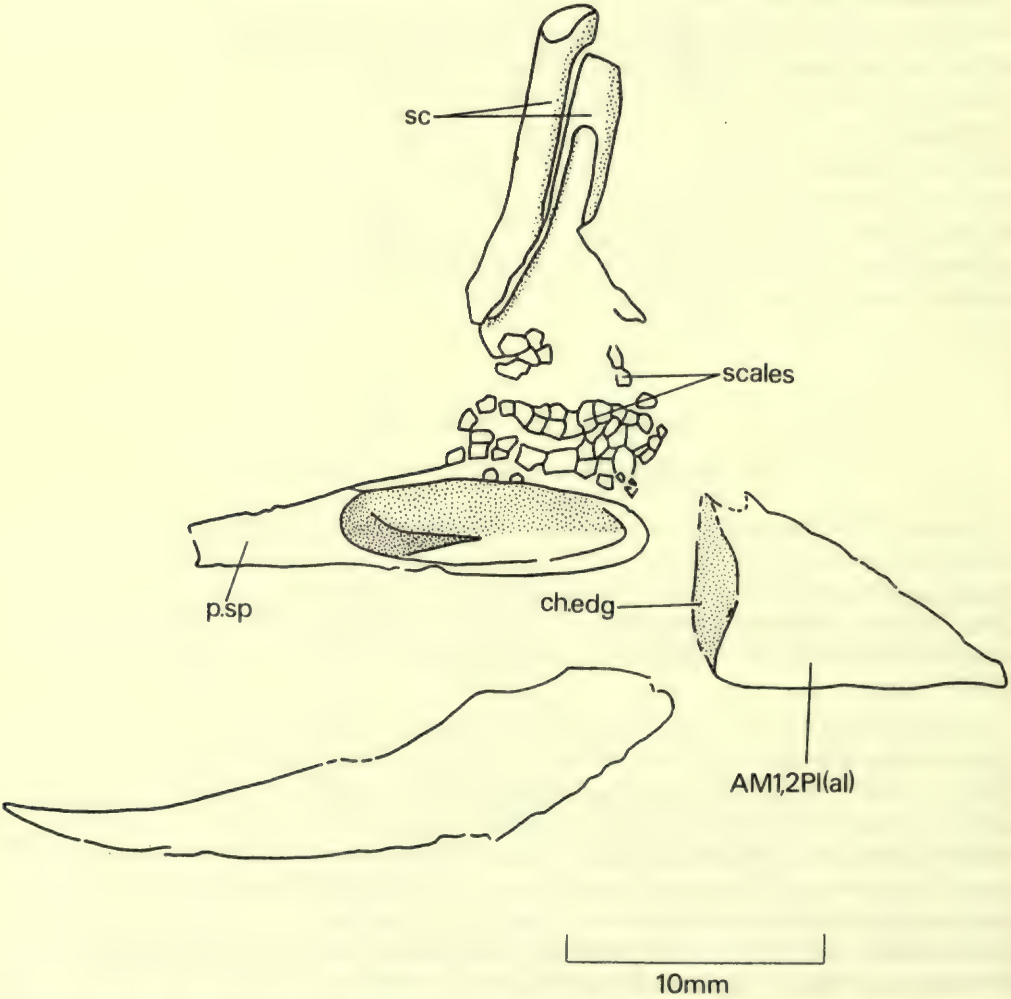
Family **EUTHACANTHIDAE**

Euthacanthus macnicoli Powrie

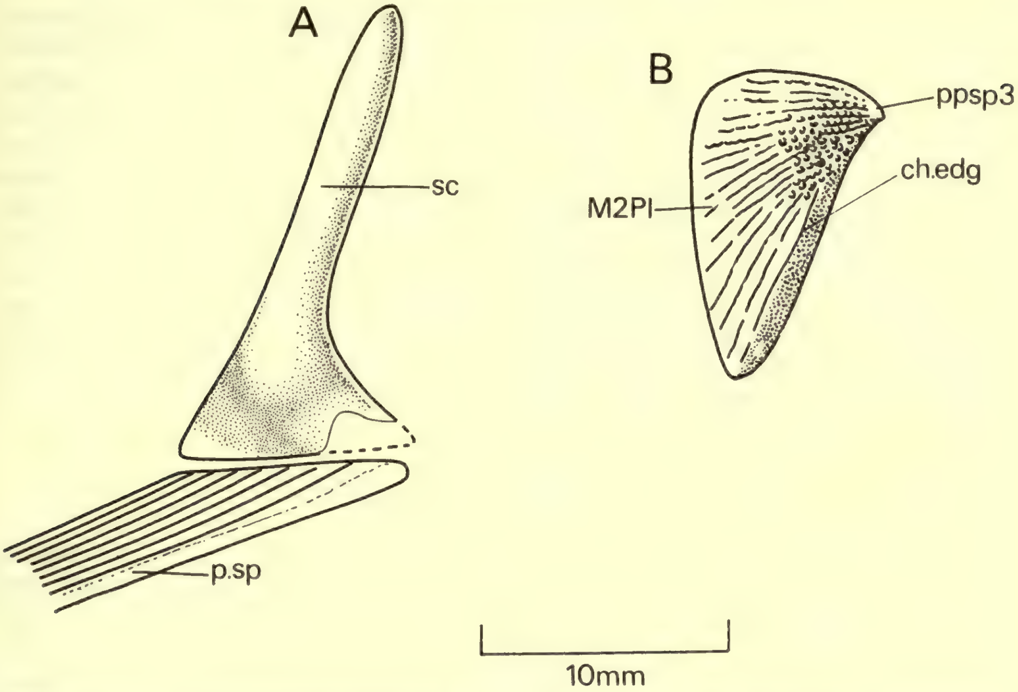
Powrie (1870) recognised five species of *Euthacanthus* in the Lower Old Red Sandstone of Scotland, but only one of these, *Eu. macnicoli*, is well known, and the classification of the genus is in an unsatisfactory state. The following account is based on the type specimen of *Eu. macnicoli* (RSM 1891.92.231 – BM P.1337, counterparts) and two others referred to this species, RSM 1887.35 and GSM 88923 (Pl. 18, fig. 2).

DERMAL SKELETON. The dermal girdle consists of a single pair of ornamented plates which are each produced laterally into a flattened, horizontal spine (Text-fig. 36B). There is no suture between the plate and the spine. Watson (1937, Text-fig. 4) interpreted each plate as a ventral element ('antero-lateral pectoral dermal bone'), but the size and relationships of the plate suggest that it should be termed the ascending lamina of the second middle pinnal plate (*M2Pl*, Text-fig. 36B), and thus the spine is paired prepectoral spine 3 (*ppsp3*). The posterolateral edge of the plate is bevelled (*ch.edg*), like the corresponding margin in *Parexus* and *Vernicomacanthus*. The ornamentation comprises large leaf-like tubercles which run in rows and tend to fuse into ridges (Pl. 18, fig. 2). The ridges become finer on paired prepectoral spine 3 and converge on its tip. The visceral surface of the lamina is unknown. No other plates are found in the girdle, and there is no evidence of other prepectoral spines, or of a pair of intermediate spines, between the bases of the ribbed pectoral spines. Watson's (1937, Text-fig. 4) restoration shows the 'first' intermediate spine (see p. 197 *infra*) more posteriorly situated, between the tips of the pectoral spines.

ENDOSKELETAL GIRDLE. The perichondral scapular ossification (*sc*) has a similar shape and extent to that of other Lower Devonian species (Text-fig. 36A). The lateral surface of the scapulocoracoid is coated with enlarged body scales which run in irregular rows. They are well seen in the type specimen (Watson 1937, Pl. 7, fig. 2), and reach about twice the size of the adjacent flank scales. They do not fuse to form lateral shoulder-girdle plates.



TEXT-FIG. 35. *Parexus recurvus* Agassiz. Lower Old Red Sandstone. Sketch of shoulder-girdle, RSM 1891.92.190. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.



TEXT-FIG. 36. *Euthacanthus macnicoli* Powrie. Lower Old Red Sandstone. A, scapulocoracoid and proximal region of pectoral spine in lateral view. B, right ascending pinnal lamina with paired prepectoral spine 3. After GSM 88923 and RSM 1887.35. Arbuthnott Group, Dundee Formation, Turin Hill, Angus, Scotland.

PECTORAL FIN. Again the endoskeleton of the fin is unknown, as are the dermotrichia. Watson (1937 : 65) records that the fin web 'is often visible as an area covered with very small square scales'. This condition is well seen (Pl. 15, fig. 1) in a specimen of unknown history in the RSM, which I have tentatively determined as *Euthacanthus* sp. Here the scales run in long, lepidotrichia-like rows, which converge on the base of the fin. They show that the web was extensive and the base relatively narrow.

Family **GYRACANTHIDAE**

The relations of gyracanthids were quite unknown until Woodward (1906) described *Gyracanthides murrayi* from the Carboniferous of Australia and showed that it was an acanthodian. For *Gyracanthus* spp. (type *G. formosus* Agassiz) and *Gy. murrayi* he erected the family Gyracanthidae, which was defined as follows: '. . . round-bodied and depressed Acanthodians, with the pectoral fins very large and the pelvic fins advanced far forwards. Dorsal and anal fins much reduced and sometimes apparently without spines'. When I published my classification of acanthodians (Miles 1966), I felt that a close relationship between *Gyracanthides* and *Gyracanthus* had not been demonstrated, and that profitable discussions of the structure and relationships of Carboniferous climatiiforms could only be based on the Australian genus. From this I was led into the error of listing *Gyracanthides* as the type genus of the family Gyracanthidae Woodward.[4] Subsequently I erected the family Gyracanthididae for this genus (Miles 1971). Further study of gyracanthids, however, has convinced me that the family Gyracanthidae should be retained in its original sense (type *Gyracanthus*), and that it is proper to refer both *Gyracanthides* and *Oracanthus* to this family. Woodward's definition may be amended to include: 'shoulder-girdle with paired prepectoral spine 3'. Because of the structure of the shoulder-girdle, the Gyracanthidae may be placed in the Climatioidei.

Gyracanthus formosus Agassiz

It is only necessary to consider the type species in this paper; it is the best known species. Traquair (1884) has discussed the paired fin-spines in some detail, and concluded incidentally that dorsal fin-spines were not present. The 'carpal bones' of Hancock & Atthey (1868) are of particular interest. Traquair (1884 : 44) correctly concluded that they were 'dermal appendages . . . situated in the neighbourhood of the pectoral fin', and pointed out that they were hollow and often badly crushed. The variation in form noticed by some authors is due partly to this crushing and partly to incomplete preservation.

One specimen (BM 45864, Pl. 21) makes the structure of the 'carpal' element clear. It is from the 'Coal Measures of Newcastle upon Tyne', and although the locality is not recorded it is probably from the Low Main Seam, Newsham. The specimen comprises a hollow, curved spine, i.e. the 'triangular bone' which is normally preserved, and a dermal plate (Text-fig. 37). No visible suture separates the spine from the plate, and the free surfaces of both are extensively ornamented with flat, fine anastomosing ridges. There are no sure means of orientating the specimen, but it appears most probable that the greater part of the plate formed a ventral lamina, and that it includes a low lateral lamina behind the spine. If this is correct, I estimate that the spine is directed posterolaterally and very slightly ventrally, with its long axis set at about 10° from the horizontal. In transverse section it is oval, and is tilted at about 45°, with its leading edge higher than its trailing edge. The wide cavity of the spine is open (*cav.sp*) and is bounded posteriorly on the visceral surface of the dermal plate by a high, stout endoskeletal ridge (*Pl.la.p*). It is most reasonable to interpret the spine as paired prepectoral spine 3, as this is the only spine invariably present in climatioids. The endoskeletal ridge may thus be compared with the posterior endoskeletal lamina in *Sabrinacanthus*. From this

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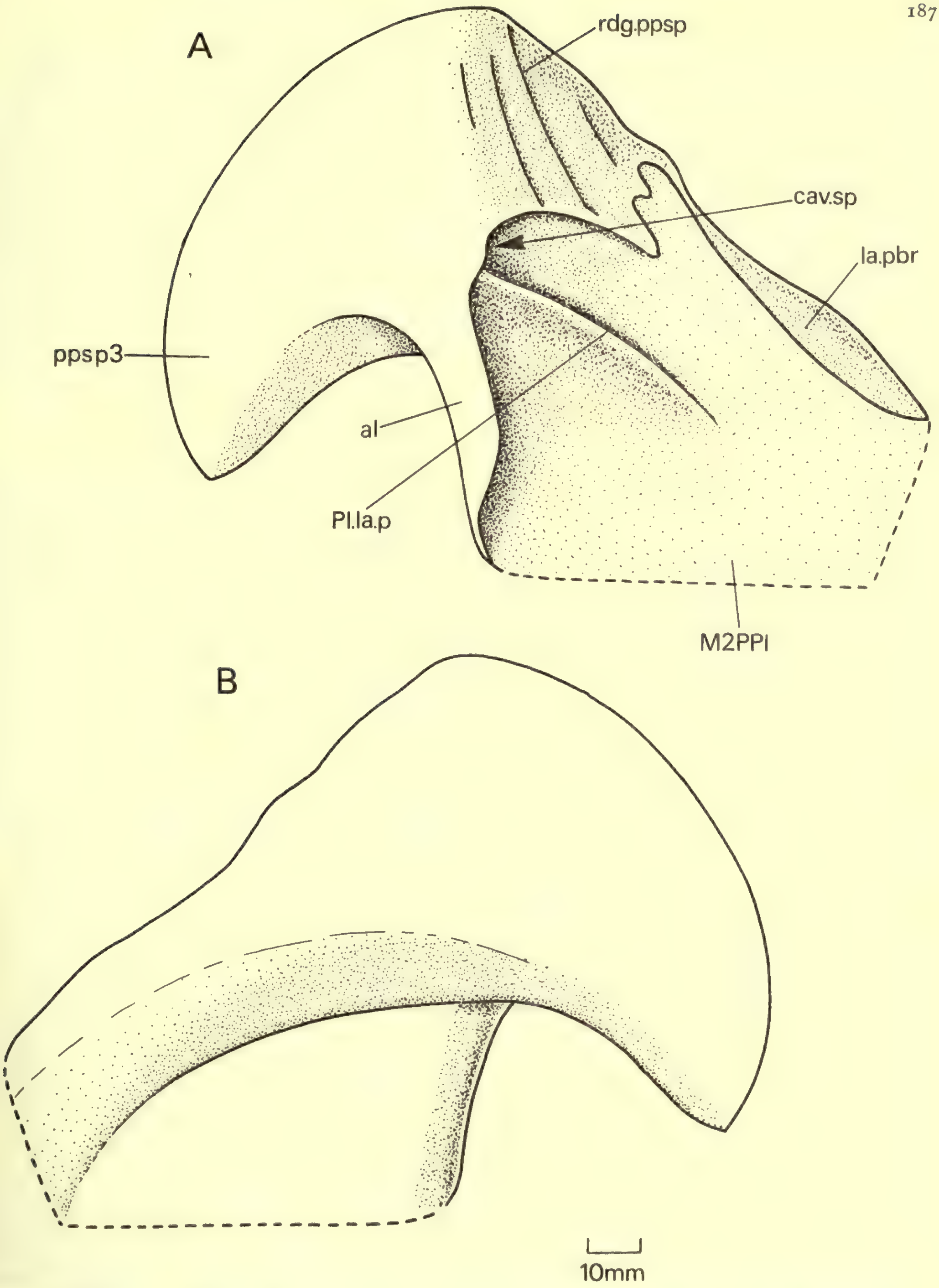
[4] I am indebted to Drs C. Patterson and D. Baird for independently bringing this mistake to my attention, shortly after the publication of my paper.


A
rdg.ppsp
cav.sp
la.pbr
ppsp3
al
Pl.la.p
M2PPl
B
10mm

TEXT-FIG. 37. *Gyracanthus formosus* Agassiz. Upper Carboniferous. Restoration of dermal plate and paired prepectoral spine 3 in A, dorsal and B, ventral view. After BM 45864. Low Main Seam, Newsham, Northumberland, England.

it follows that the dermal plate comprises the second middle pinnal and a much reduced posterior pinnal plate, despite its lack of contact with the pectoral spine. The anteromesial and lateral margins of the plate are raised, and form low postbranchial (*la.pbr*) and ascending (*al*) laminae respectively. Both laminae merge smoothly with the prepectoral spine, and the first bears a series of broad, low ridges separated by narrow grooves (*rdg.ppsp*). The presence of an ascending lamina posterior to the spine is unusual in comparison with Devonian climatioids.

There can be no doubt that the spine and plate just described were carried immediately in front of the pectoral spine and main parts of the scapulocoracoid. Unfortunately this last structure and the pectoral fin are unknown. There is no evidence of additional prepectoral or intermediate spines.

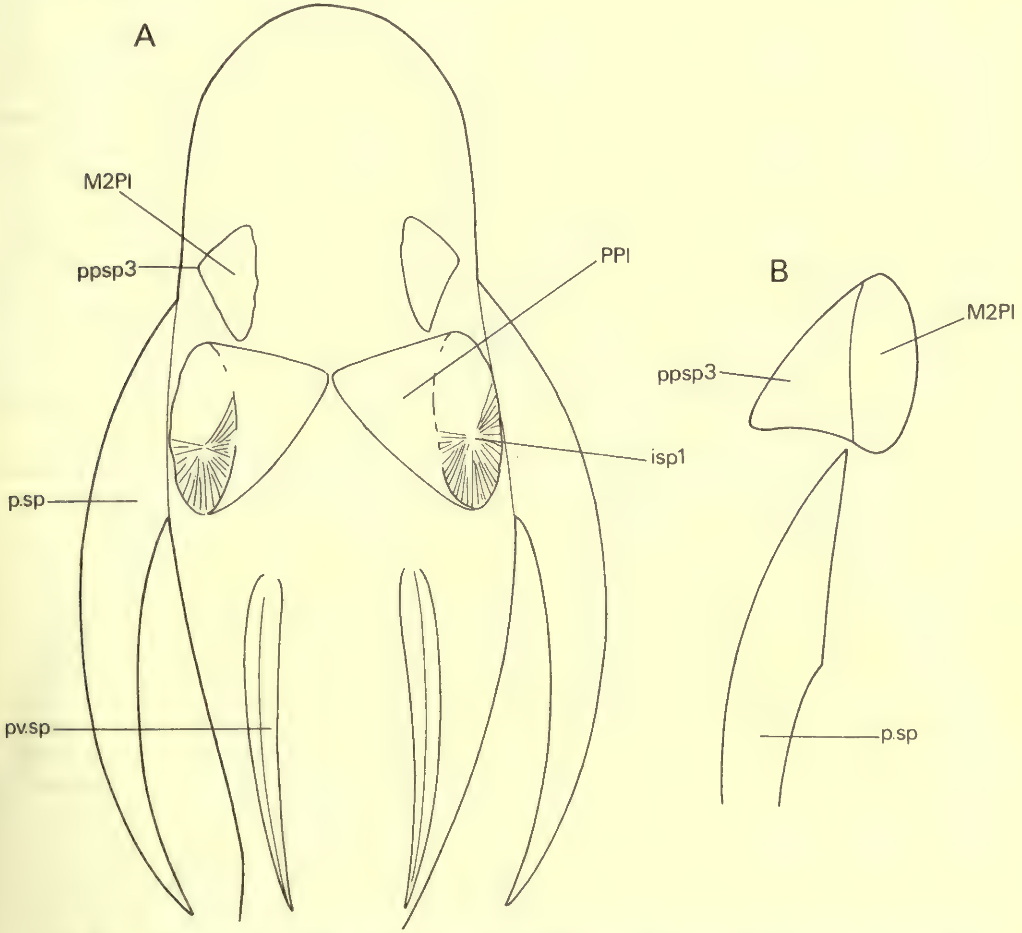
Gyracanthides murrayi Woodward

Woodward summarised his conception of this species in a single restored drawing (1906, Text-fig. 1). If we assume that this figure is correct, *Gyracanthides* exhibits long, curved pectoral spines (*p.sp*, Text-fig. 38A), between which lie triangular posterior pinnal plates (*PPl*; 'basal plate') which carry the first intermediate spines (*isp1*; 'posterior free pectoral spine'). Immediately in front of these structures is a separately developed paired element which might be interpreted as the second middle pinnal plate (*M2Pl*) plus paired prepectoral spine 3 (*ppsp3*; 'anterior free pectoral spine'). There are no other intermediate spines and the pelvics (*pv.sp*) lie relatively far forwards.

In some respects this restoration is strange, and the shoulder region bears little relationship to that of *Gyracanthus*. The presence of a free-lying posterior pinnal plate is particularly odd, as this is a characteristic of diplacanthoids (p. 201; Text-fig. 39A), and it suggests that *Gyracanthides* is incorrectly referred to the climatioids. However, there are grounds for believing that Woodward's restoration is incorrect.

Hills (1958 : 91) has stated that the 'anterior free pectoral spines' in the restoration are based on the tooth-plates of '*Ctenodus*' *breviceps*. This comment presumably applies to the details in Woodward's figure, and it is also likely that some detached elements have been wrongly determined, but there can be no doubt that the hollow structures termed 'anterior free pectoral spines' in the articulated specimens really belong to *Gyracanthides*. A more important point is that none of the articulated specimens shows a full set of anterior and posterior 'free pectoral spines', and that the spines are always somewhat displaced. Thus the type specimen (Woodward 1906, Pl. 1, fig. 1) shows one 'anterior free spine' and the 'oval plate closing base of posterior free pectoral spine'; another specimen (Pl. 1, fig. 7) shows only one 'free spine', termed the anterior, which is mesial to the proximal end of the pectoral spine; and yet another specimen (Pl. 2, fig. 1) shows one 'posterior free pectoral spine', situated mesial and slightly posterior to the pectoral spine. There is no direct evidence, therefore, that *Gyracanthides* had both anterior and posterior 'free pectoral spines', and Woodward's (1906 : 2, 6, 7) restoration seems to have been based on comparisons with Scottish Devonian species, then imperfectly understood.

Woodward compared the 'posterior free pectoral spines' with the triangular spines (paired prepectoral spine 3; *ppsp3*) of *Gyracanthus*. This is evidently correct, and the 'basal plate' may thus be said to include the second middle pinnal plate (*M2Pl*). Both structures must, however, have been more anteriorly situated than in the original restoration, in a prepectoral position. The 'anterior free pectoral spines' appear to be based on a misinterpretation of the same structures, and have in fact no real existence. This is supported by the type specimen in which the single 'anterior pectoral spine' is of similar size to the 'posterior pectoral spine', although according to the written description (Woodward 1906 : 7, 8) the anterior spine should be much smaller than the posterior.



Text-fig. 38. *Gyracanthides murrayi* Woodward. Lower Carboniferous. A, Sketch restorations to show shoulder-girdle in ventral view, according to Woodward 1906, Text-fig. 1. B, new interpretation of dermal plate and spines of right side.

A tentative new plan of the shoulder region is given in Text-fig. 38B. This allows a direct comparison to be made with *Gyracanthus*, to which *Gyracanthides* may be closely related. The scapulocoracoid and pectoral fins are unknown.

Oracanthus milleri Agassiz

In a recent review of *Oracanthus*, Patterson (1965 : 151–152) has concluded that the genus may contain paired spines of acanthodians, and he has provided histological evidence in support of this view. The same conclusion is implicit in Woodward's (1906 : 8, 9) comparisons between the triangular ('posterior free pectoral') spines of *Gyracanthus*, *Gyracanthides* and *Oracanthus*. This conclusion suggests that the long spines of *O. milleri* are pectoral fin-spines (e.g. Davis 1883, Pl. 64, fig. 2; also *O. postulosus*, Pl. 65, fig. 1), and the short triangular spines (Davis 1883, Pl. 63, figs 1–3) are prepectoral spines. The latter were presumably carried in front of the pectoral spines, as in *Gyracanthus* and *Gyracanthides*, and are paired prepectoral spines (no. 3). There is, however, no evidence of a pinnal plate, and the whole pinnal series may have been entirely reduced. Davis's three specimens of the prepectoral spine are preserved in the British Museum (Nat. Hist.) (P.2873, P.2874, P.2875). They are hollow, ornamental structures that have been accurately figured, making it possible to discount the misleading written description (Davis 1883 : 530). One point of interest is the bevelled margin, which invites comparison with the posterolateral margin of the ascending pinnal lamina-paired prepectoral spine 3 complex of *Euthacanthus* (see also *Parexus*, *Vernicomacanthus*). The nature of the other dermal bones which have been ascribed to *Oracanthus* (Davis 1883; Patterson 1965) remains unknown.

There now seems to be sufficient evidence to refer *Oracanthus* to the Gyracanthidae, although its close affinities remain undisclosed for the want of better material.

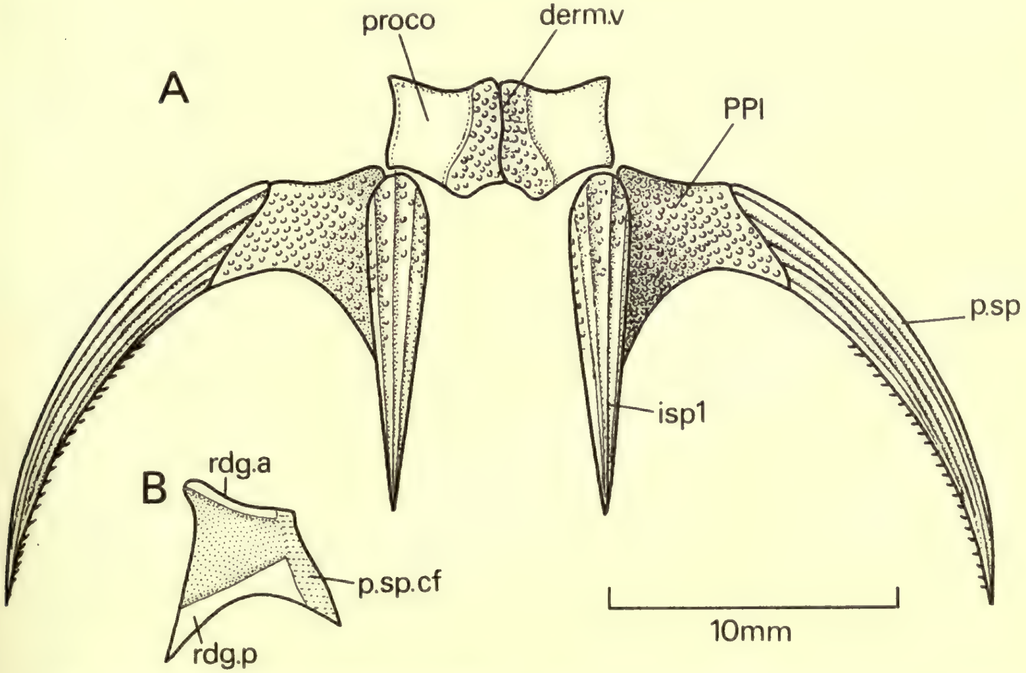
Suborder DIPLACANTHOIDEI

Family **DIPLACANTHIDAE**

Diplacanthus striatus Agassiz

Gardiner (1966 : 50) believes that the correct name for this species is *Diplacanthus crassissimus* Duff, but for reasons already given (Miles 1966 : 166, footnote 2) I retain the widely used name *D. striatus*. It is the type and best known species of *Diplacanthus*, and the only one which it is necessary to consider here. Other species appear to be almost identical in the structure of the shoulder-girdle. Woodward (1891, Text-fig. 3) and Watson (1937 : 94, Text-figs 15, 16) have described the girdle (also Traquair 1894a), but their accounts do not always agree, and some points remain to be added. The following account is based on BM 36582, P.1357a, P.1366, P.1364–4311 (counterparts) and RSM 1891.92.334 from the Middle Old Red Sandstone of Tynet Burn, Banffshire, Scotland, and casts of HU MB26 (Miles 1966, Text-fig. 10) which is believed to be from the same locality.

Dermal skeleton. If a comparison is made with climatioids, the dermal skeleton (Text-fig. 39) is represented solely by the posterior pinnal plate (*PPl*; 'basal cartilage', Woodward 1891; 'dermal plate', Watson 1937). Certain other dermal structures are considered below together with the scapulocoracoid. The posterior pinnal is arched so that the pectoral spine (*p.sp*) is carried above the base level, and the anterior margin turns up to contact the postbranchial lamina of the scapulocoracoid. Laterally the plate overlaps a narrow area at the base of the pectoral spine (Watson 1937 : 94; Miles 1966, Text-fig. 10), so that the two structures normally remain firmly united. Mesially the plate abuts against the large first intermediate spine (*isp1*; 'median spine', Woodward 1981; 'admedian pectoral spine', Watson 1937; 'ventral spine from shoulder girdle', Miles 1966). There is no evidence that these elements overlapped each other. Watson (1937 : 94) suggests that the dermal plate spreads mesially around the base of the first intermediate spine, but I have not been able to confirm this with the Tynet specimens, and do not show this condition in my restoration. The outer surface is ornamented with numerous fine, irregularly arranged

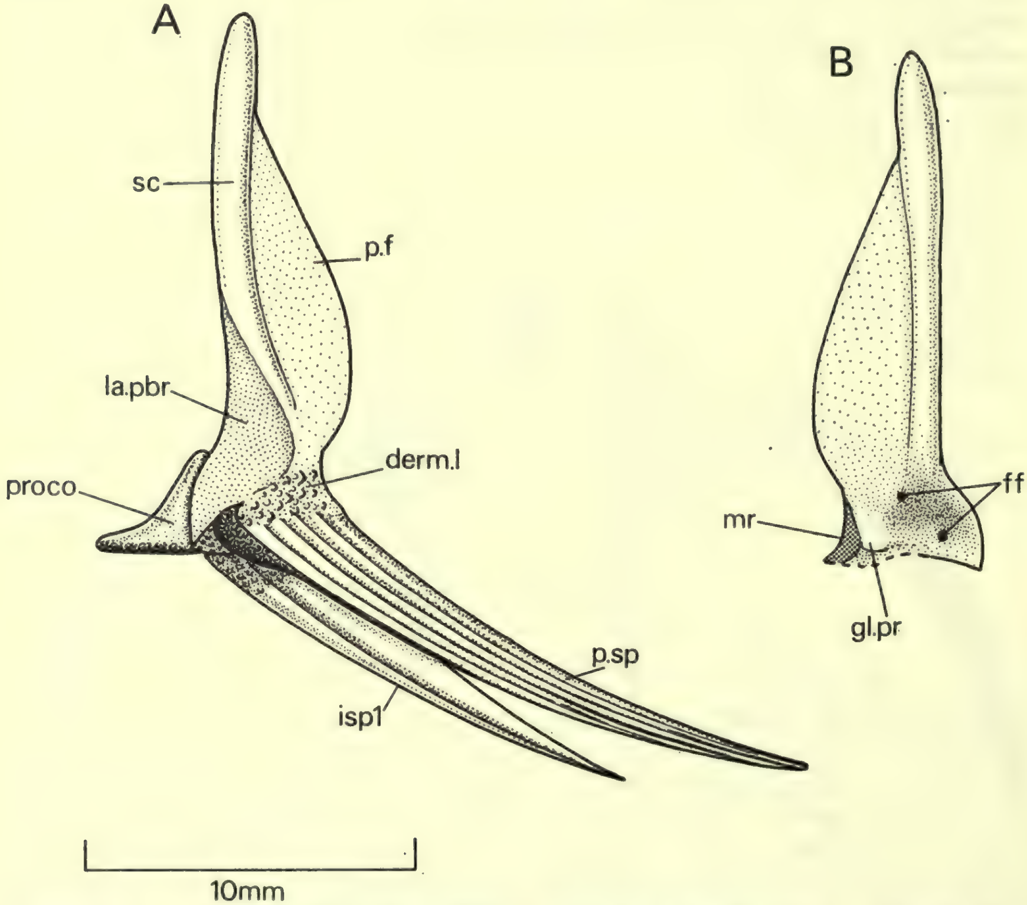


Text-fig. 39. *Diplacanthus striatus* Agassiz. Middle Old Red Sandstone. A, restoration of shoulder-girdle in ventral view; B, dorsal view of posterior pinnal plate. After BM 36582, P.1357a, P.1366, P.1364–4311 (counterparts). Tynet Burn, Banffshire, Scotland.

tubercles. The visceral surface has a smooth area laterally (*p.sp.cf*, Text-fig. 39B) for the overlap surface of the pectoral spine, and anterior and posterior ridges (*rdg.a*, *rdg.p*) which delimit a central area for the base of the unossified coracoid. These ridges are together homologous with the posterior pinnal ridge of *Climatius*, and the anterior probably received the base of a posterior endochondral lamina (cf. *Sabrinacanthus*).

The pectoral and first intermediate spines are already well known, and can be seen in the illustrations. They require no further comment.

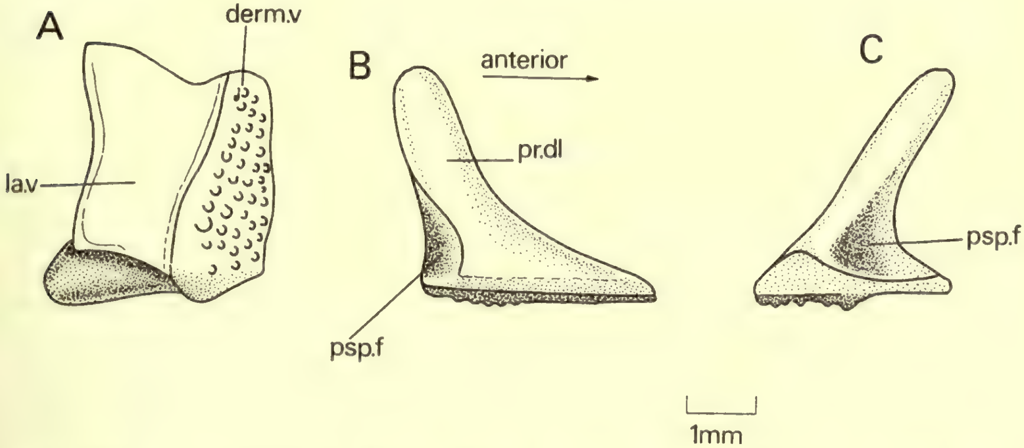
Endoskeletal girdle. The endoskeleton (Text-fig. 40) consists of the perichondrally ossified scapular blade (*sc*) and a separate procoracoid (*proco*). The scapula ('clavicle', Woodward 1891) comprises a vertically standing shank, with a



Text-fig. 40. *Diplacanthus striatus* Agassiz. Middle Old Red Sandstone. A, restoration of shoulder-girdle in lateral view; B, scapula in mesial view. Mainly after RSM 1891.92. 334, and Watson 1937, Text-fig. 15. Tynet Burn, Banffshire, Scotland.

thin posterior flange (*p.f*) and a less-extensive, inflected postbranchial lamina (*la.pbr*). The base of the lateral surface is ornamented (*derm.l*, Text-fig. 40A; Miles 1966, Text-fig. 10), apparently because some body scales have fused with each other and with the girdle, to form a lateral dermal component. This lies immediately above the base of the pectoral spine, which is firmly attached to (perhaps overlapped by) the girdle, and it is not easy to decide exactly where the girdle and spine meet in articulate specimens. The postbranchial lamina may include part of the coracoid process, if this structure is not wholly represented by the procoracoid; ventrally it lies in contact with the anterior ridge of the posterior pinnal plate. In BM P.1364–P.4311 and RSM 1891.92.334 there is some indication that the base of the posterior flange of the scapula projects mesially, near the posterior margin, as a glenoid process (*gl.pr*). This is shown somewhat diagrammatically in Text-fig. 40B, and the incompletely ossified posterior surface of this process is represented as a margo radialis (*mr*). The determination of this process is supported by its position, immediately mesial to the base of the pectoral spine. If it is correct, it indicates that the scapula of *Diplacanthus* includes a perichondrally ossified region homologous with the dorsal part of the middle region in *Acanthodes*.

The procoracoid (*proco*, Text-figs 39A, 40A, 41) has been differently interpreted by Woodward (1891, 'infraclavicle') and Watson (1937, 'coracoid'; also Miles 1966). Woodward regarded it as a membrane bone, presumably because of its ornamentation, whereas Watson believed that it was an endoskeletal bone laid down round a cartilage, because of its calcite filling. The evidence of both of these workers is valid, and it is here interpreted to show that the perichondral procoracoid had a dermal element fused to its ventral surface. I have studied the bone by means of silicone-rubber replicas (Text-fig. 41), obtained by treating negatively prepared



Text-fig. 41. *Diplacanthus striatus* Agassiz. Middle Old Red Sandstone. Right procoracoid in A, ventral, B, lateral, and C, posterior views. After BM P.1364–4311 (counterparts). Tynet Burn, Banffshire, Scotland.

BM P.1364–4311 as a two-piece mould. The perichondral bone comprises a flat ventral lamina (*la.v*) with a high, dorsomesially directed process (*pr.dl*). The posterolateral face of the base of this process is hollowed into a distinct fossa (*psp.f*), which in the articulated girdle lies immediately in front of the basal opening of the first intermediate spine. The mesial margin of the ventral lamina lies in contact with the procoracoid of the other side, possibly in a butt-joint. Thus the two halves of the girdle are united in the middle line. The precise relationship of the procoracoid to the rest of the girdle is less easy to determine. Possibly the posterior margin of the ventral lamina abutted laterally against the base of the first intermediate spine, and it seems clear that the dorsal process rested in some way against the mesial edge of the postbranchial lamina of the scapula. Although the details of this last relationship are unknown, it is obvious that the connexion was not as highly evolved as in *Acanthodes*. It is germane to note, therefore, that the pectoral spine is fixed in *Diplacanthus*, and not mobile as in *Acanthodes*.

The dermal component (*derm.v*) is restricted to the mesial half of the lower face of the procoracoid (Text-fig. 41A). This element is paired and not easy to compare with the plates of climatioids. Topographically, both members of the pair might be compared with the median posterior lorical plate of *Climatius*, only this last plate is not associated with any part of the scapulocoracoid. An alternative comparison with one of the paired middle pinnal plate also founders, because these plates are laterally situated, in front of the posterior pinnal, and do not meet their fellows in the middle line. Therefore, I conclude that the dermal component of the procoracoid in *Diplacanthus* is a new element without a homologue in climatioids. It is comparable with the element attached to the lateral surface of the scapula, and was probably formed by the fusion of scales.

PECTORAL FIN. No remains of this structure have been found, apart from the 'ceratotrichia' figured by Watson (1937, Text-fig. 15, Pl. 10, fig. 1) in RSM 1891.92.334. Traquair's (1896, Pl. 2, fig. 1) restoration of the fin is, however, probably correct in principle.

Rhadinacanthus spp.

Traquair (1888 : 512) referred *Diplacanthus longispinus* Agassiz to the new genus *Rhadinacanthus*, because he believed it to lack 'the second or lower pair of intermediate spines' (i.e. the first intermediate spines). Woodward (1891 : 26), however, pointed out that these spines occur in their usual position in BM P.4041 from the Middle Old Red Sandstone of Gamrie. I have been able to confirm this in Woodward's specimen, and in other specimens from Scotland; and the spines can also be seen in the holotype (BM P.6756) of *Rhadinacanthus horridus* (Woodward) from the early Upper Devonian Escuminac Formation of Canada (Woodward 1892b; Russell 1951). Traquair (1896 : 244) appears to have accepted Woodward's point, but nevertheless retained the genus *Rhadinacanthus*. ('Distinguished by its long slender spines and its sharply and beautifully sculptured scales'.) On the evidence of the type species, *R. longispinus*, this genus can be most readily separated from *Diplacanthus* by the peculiar fact that the second dorsal fin-spine is longer than the first.[5] It is not yet possible to decide whether this is also true of *R. horridus* (cf. Woodward 1892b : 482; Russell 1951).

The shoulder-girdle is comparable in all respects in *Diplacanthus* spp. and *Rhadinacanthus* spp. Two comments only are required. In BM P.43276 (*R. longispinus*), from the Middle Old Red Sandstone of Tynet Burn, there are two small foramina on the inner face of the scapulocoracoid, which may together equal the subscapular foramen of *Acanthodes bronni*. They have been entered in the drawing of *Diplacanthus striatus* (*ff*, Text-fig. 20B). Russell (1951 : 405–406) writes that there is a 'restricted membrane joining lateral and admedian spines', but there is no evidence of a web between the pectoral and first intermediate spine in any acanthodian I have examined, and this statement may be wrong.

IV. THE EVOLUTION OF THE CLIMATIOID SHOULDER-GIRDLE

In the foregoing review of structure I have accepted that the paired fin-spines and the paired prepectoral and intermediate spines are serial homologues. Whether the median prepectoral spine represents an additional pair of elements in this series, which have come together in the middle line, is unknown, and it is not considered in this discussion. I have further hypothesised that there is fundamentally a one-to-one correspondence between the paired dermal plates and prepectoral spines in the shoulder-girdle. This segmentation is probably also expressed in the ventral part of the scapulocoracoid, in the form of vertical endochondral lamellae placed subtransversely across the cartilage of the girdle. At the moment, however, useful information about these lamellae is only found in *Climatius* and *Sabrinacanthus*, and an element of doubt remains about their significance. There is no evidence bearing on the exact segmental arrangement of the spines, other than their regular disposition in genera such as *Erriwacanthus* (Text-fig. 27).

From the one-to-one correspondence hypothesis of plates and paired spines it should follow that the posterior pinnal plate is more complex than I have so far indicated, as it is associated with both the pectoral and first intermediate spine. However, there is no evidence that it is a compound plate. I suggest, therefore, that the pectoral spine became displaced laterally (p. 207) before the (phylogenetic) formation of the dermal girdle, as it has this position in ischnacanthiforms and acanthodiforms, and that the first intermediate spine became displaced forwards and secondarily associated with the posterior pinnal plate as a subsequence to this event. The one-to-one correspondence hypothesis also implies that the primitive climatioid shoulder-girdle had a full set of prepectoral spines and well-developed dermal plates, and that these structures were reduced during the evolution of the group. This might be expected as the reduction of the exoskeleton is a general trend in the evolution of many early groups of armoured fishes. The stratigraphical occurrence of climatioids does not weigh against this suggestion. There is evidence of up to three paired prepectoral spines, and this has been taken as the maximum number in the construction of a hypothetical primitive climatioid shoulder-girdle (Text-fig. 42). These spines are associated with the anterior, first and second middle pinnal plates; and the pectoral and first intermediate spines are associated with the posterior pinnal plate. I have also assumed that anterior and posterior lorical plates are present, and that the former is associated with the median prepectoral spine.

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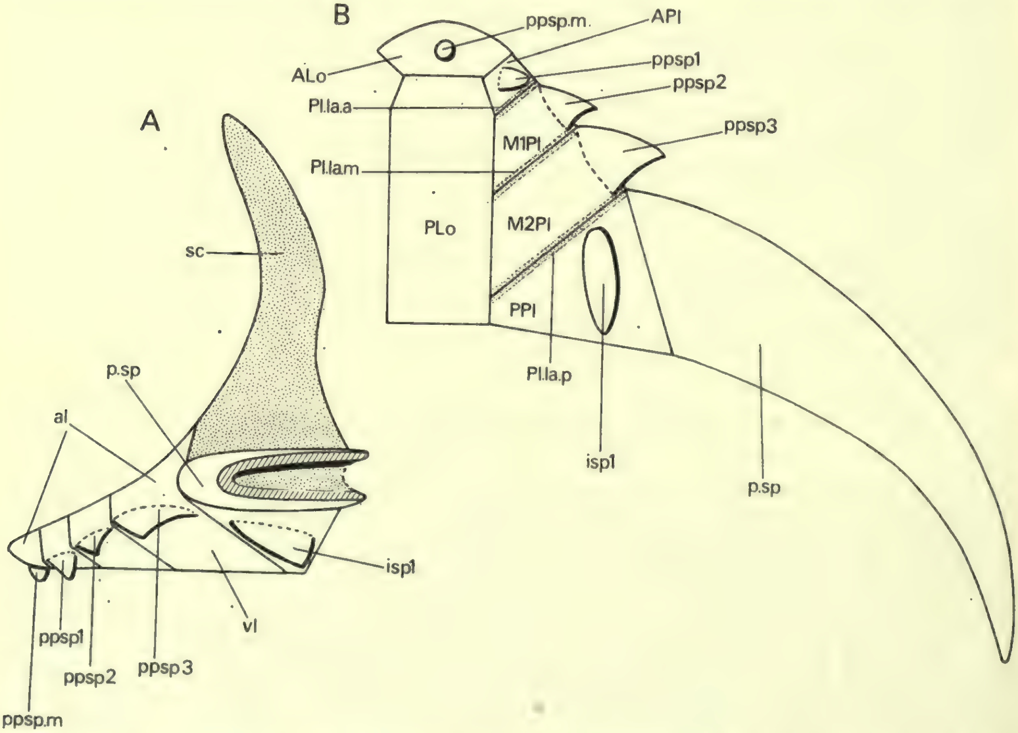
[5] I am indebted to Professor F. H. Stewart (pers. comm., Dec. 1964) for bringing this point to my notice.

If the dermal shoulder-girdle of climatioids has evolved from a primitive structure of the type shown in Text-fig. 42, it is legitimate to seek interspecific homologies in the case of both the spines and plates. There is after all no reason to question the monophyly of climatioids. This stands in contrast to the problem of the intermediate spines. These are sets of homonomous (serially homologous) structures, but there are no ways of drawing safe interspecific homologies, except in the case of the first intermediate spine which is primitively included in the shoulder-girdle and normally retains an anterior position adjacent to the base of the pectoral spine. The remaining intermediate spines have been numbered separately in each species, with



Text-fig. 42. Hypothetical primitive climatioid shoulder-girdle in A, lateral and B, ventral view. In A the scapulocoracoid is stippled and in B the positions of the internal endochondral lamellae are shown by bands of fine stipple.

the true first spine usually omitted from the counts (p. 164). Thus there are no means of demonstrating, e.g. that the second spine is homologous throughout climatioids. I might stress in passing that the 'first intermediate spine' of *Euthacanthus* (p. 184, Watson 1937, Text-fig. 4) stands some way behind the shoulder-girdle, and is almost certainly incorrectly determined.

The spines and dermal plates are variously reduced and lost among climatioids. I have concluded that a plate may persist following the loss of its spine (e.g. the anterior pinnal in *Brachyacanthus*, *Parexus* and *Vernicomacanthus*), but I have found no evidence of a prepectoral spine surviving after the loss of its pinnal plate, except in the poorly understood genus *Oracanthus*. This may be contrasted with the survival of the first intermediate spine (and pectoral spine) in the cited Old Red genera, following the loss of the posterior pinnal plate. The first intermediate spine appears, however, to have been completely suppressed among euthacanthids and gyracanthids.

It has proved difficult to determine the paired prepectoral spines in species in which they have been reduced from the primitive number of three. Paired prepectoral spine 3 seems generally to have been retained and as a rule is readily fixed. The reasons for other spine determinations have been given in the above accounts. Each case has been treated on its merits, but nevertheless the final results appear to be somewhat arbitrary. I have considered other interpretations, e.g. by applying the hypothesis that the paired prepectoral spines became reduced in a uniform sequence, such as in the order 2, 1, 3. But to my mind these have led to less convincing determinations than those presented in this paper.

A question quite distinct from the primitive extent of the exoskeletal shoulder-girdle concerns the primitive organization of this structure, particularly of its superficial layers. The exoskeleton of the pinnal plates described above exhibits four different states.

(1) The pinnal plates are fused together into a single structure with an undivided, ornamented surface (e.g. *Erriwacanthus falcatus*, *Sabrinacanthus*, *Vernicomacanthus*, *Parexus*).

(2) The pinnal plates are present as separate, thin, deeply-seated sheets of bone covered by mosaics of superficial, scale-like elements (*Climatius reticulatus;* see also comments on *Ptomacanthus anglicus*, p. 175).

(3) The pinnal plates are fused together basally into a single structure, but the superficial layer is divided into a mosaic of scale-like elements (*Erriwacanthus manbrookensis*).

(4) Discrete (including compound) pinnal plates are present, each with an undivided, ornamented surface (*Brachyacanthus*).

Erriwacanthus manbrookensis and *Brachyacanthus* are poorly known forms, and some doubt attaches to the exactness of paragraphs 3 and 4, particularly with respect to *Brachyacanthus*. The following discussion, therefore, is based on *Erriwacanthus falcatus* and *Climatius reticulatus*, and these species are judged to be sufficient for most of the points that have to be made. Both show primitive characters in the number of plates and prepectoral spines. *E. falcatus*, as far as it is known, cannot be separated from a hypothetical primitive climatioid (Text-fig. 42), whilst *C. reticulatus* differs only in the loss of paired prepectoral spine 2 and the first middle pinnal plate.

It is possible that the copinnal condition of *E. falcatus* is primitive, and that it was succeeded morphologically by a series of stages in which the copinnal became divided into separate pinnal plates, which were then reduced and lost in divers ways. However, it is also possible that the copinnal plate is found only in well grown individuals, and that younger specimens of *E. falcatus* had either separate, ornamented pinnal plates; or separate, deeply-seated, scale-covered pinnal plates as in *C. reticulatus*; or a compound basal plate with a divided superficial layer, as in *E. manbrookensis*. That is, the copinnal arose by bone fusions at a late stage of growth. Changes during growth of this nature are believed to have taken place in amphiaspid heterostracans (Obruchev 1967) and rhenanid placoderms (Westoll 1967 : 91). Indeed it is not impossible that *E. falcatus* passed successively through stages resembling *C. reticulatus* and *E. manbrookensis* during skeletogenesis. Ørvig (1967 : 139) regards the copinnal condition as probably 'a product of fusion' in phylogeny, and therefore as specialised relative to the condition in *C. reticulatus*, although he has not attempted to test this view. This hypothesis is unlikely in view of the general regressive evolution of the dermal skeleton in climatiiforms.

The condition of *C. reticulatus* with separate scale-like elements, apparently representing the superficial layers of the plates, has a parallel in rhenanid placoderms. In this group the tesserate condition has been regarded as primitive by Gross (1959), and as derived, by the regressive development of the armour, by Stensiö (1963). Westoll (1967 : 91–93), however, has argued that the mere fact of the existence of the tesserate condition gives no information about the direction of morphological change, which he attempted to deduce from a sequence of fossils. Westoll lists 'the development of separate thin tesserae, which may apparently become attached to underlying flanges of dermal bones' as one of 'several processes of dermal skeletogenesis in these forms'.

If the results of Westoll's analysis of skeletogenesis in rhenanids and psammosteid heterostracans are applied to *C. reticulatus* (and *E. manbrookensis*) they suggest that this species does not differ fundamentally from other climatioids in the tesserate condition of the exoskeleton, and cannot be said, without independent evidence, to be primitive or advanced in this character. It might be possible to compare the prepectoral–intermediate spines of the girdle with the raised centres of the plates on which the tesserae develop in psammosteids and rhenanids, and thus carry further the analogy between the development of the tesserae in these disparate groups.

The above discussion may be summarised as follows. *E. falcatus* and *C. reticulatus* are primitive climatioids in the shoulder-girdle because of the extent of the dermal skeleton and number of prepectoral spines. It is not possible definitely to say which is the more primitive in the form of the skeleton (as distinct from the number of plates and spines), or that either is more primitive in this respect than other Lower Devonian genera. The extrapolation of trends of change (*v.infra*) derived from other genera suggests, however, that a primitive adult condition is with a thick, compound pinnal plate, with an undivided, ornamented surface, and with two thick, ornamented lorical plates. *E. falcatus* may approach this condition closely. *E. manbrookensis* and *C. reticulatus* may be derived from this primitive condition either by deviation in skeletogenesis, or by bone reduction in the superficio-basal direction resulting in fragmentation; or either species may be at an antecedent stage and therefore still more primitive. With respect to the ornamented surface, I favour the first of these explanations, and it is interesting to recall in this connexion the growing body of evidence to suggest that there was a marked degree of morphological independence between the superficial and basal layers of the exoskeleton in ancient armoured fishes (Westoll 1967; Ørvig 1968). This explanation would also seem to account best for the differences in the basal layer of the skeleton.

The discernible tendencies in the evolution of the climatioid dermal shoulder-girdle may now be summarised. They are concerned with the reduction of the plates and spines, which seems very generally to have taken place in the following order:

(1) The loss of the posterior pinnal plate with the freeing of the pectoral and first intermediate spines.

(2) The loss of the posterior lorical plate.

(3) The loss of the ventral laminae of the anterior and middle pinnal plates.

(4) The loss of the anterior lorical plate and median prepectoral spine.

(5) The reduction of the ascending pinnal lamina and loss of paired prepectoral spines 1 and 2.

(6) The loss of the first intermediate spine.

Other than the pectoral spine, these changes result in the retention of the second middle pinnal and paired prepectoral spine 3 as the only dermal elements in euthacanthids, and the prepectoral spine alone among gyracanthids (*Oracanthus*). Their functional significance can best be explained by the assumption that they are correlated with the development of mobile pectoral spines (p. 207).

Some morphological relationships are worth noting. The posterior pinnal is related to the base of the coracoid, which it exactly matches in shape. The whole pinnal series (see e.g. the copinnal of *Erriwacanthus falcatus*) has a similar form and extent to the coracoid plus coracoid process (see e.g. *Sabrinacanthus*, *Ptomacanthus*), and primitively these areas of the exoskeleton and endoskeleton may have had a morphogenetic relationship, which can possibly be explained in terms of the Delamination Theory (Jarvik 1959). However, in ischnacanthiforms and acanthodiforms the coracoid and coracoid process (or procoracoid) developed in the absence of a dermal skeleton, and are readily comparable with the corresponding regions in climatioids. The posterior lorical lies under the pericardium and primitively may have protected the heart; and together with the anterior lorical it held the two halves of the girdle together rigidly. The protection of the heart may have been important in early genera which rested on the bottom, although acanthodians appear principally to have been a nektonic group. With respect to the second function it is possible that the loss of both the posterior lorical and posterior pinnal plates is correlated with the development of a mobile pectoral spine, and the acquisition of a less rigid girdle. The long coracoid processes of *Ptomacanthus* may well have been held together in the middle line by ligaments, as the median plates appear to be reduced in this genus (p. 175).

Erriwacanthus is wholly primitive in the characters it exhibits, and its relationships cannot be determined. Of the Scottish climatiids, *Climatius* is the most primitive genus and its nearest relative is undoubtedly *Brachyacanthus*. Although the features they share in the shoulder-girdle which are not found in the other genera (presence of a discrete posterior pinnal and possibly a posterior lorical) could both be interpreted as primitive, this relationship is supported by a far-reaching identity of structure in the head skeleton and body (Watson 1937). *Brachyacanthus* is specialised relative to *Climatius* in the loss of paired prepectoral spine 1, the apparent fusion of the anterior and second middle pinnal plates, and the reduction or loss of the posterior lorical; it is not known whether the median prepectoral spine was present.

A collateral line of descent to that of *Climatius* and *Brachyacanthus* among Scottish climatiids includes *Parexus* and *Vernicomacanthus* (*V. uncinatus*), although the common ancestor of these lines must have been more primitive than *Climatius* and possessed paired prepectoral spine 2. *Parexus* and *Vernicomacanthus* resemble each other in the loss of the ventral pinnal laminae and posterior lorical plate, and in the fusion of the ascending laminae of the anterior and first and second middle pinnal plates. It is possible that these resemblances are the result of parallel evolution from an *Erriwacanthus*-like common ancestor, but this possibility may reasonably be ignored till evidence is produced that demands its consideration. No such evidence is forthcoming from the shoulder-girdle or from the exoskeleton of the head.

The relationships of the English climatiids *Sabrinacanthus* and *Ptomacanthus* are less easy to determine, although I have some confidence in the hypothesis that *Ptomacanthus* belongs to the *Climatius-Brachyacanthus* side of the above division. *Ptomacanthus* resembles *Climatius* in the number and disposition of the prepectoral spines, in particular in the loss of paired spine 2 and the first middle pinnal plate, and in the scale-like condition of the ornamented surface of the remaining pinnal plates. The pinnal plates are, however, not discrete structures, and *Ptomacanthus* may be more advanced than *Climatius* and *Brachyacanthus* in the loss of the posterior lorical plate (and the first intermediate spine? See p. 122). I suggest that *Ptomacanthus* is more closely related to *Climatius* than to *Brachyacanthus*, but at the present time this cannot be tested.

Sabrinacanthus shows many primitive characters. It is advanced relative to a hypothetical primitive climatioid (Text-fig. 42), in the loss of paired prepectoral spine 1 and the corresponding anterior pinnal plate. This specialisation would be unexpected in the common ancestor of the two lines of Scottish genera considered above, and it suggests that *Sabrinacanthus* is equally distinct from both lines.

Euthacanthus resembles *Parexus* and *Vernicomacanthus* in the complete reduction of the posterior lorical plate and ventral pinnal laminae. *Euthacanthus* is more advanced than these genera, however, in the further loss of the anterior lorical, the median prepectoral spine and the anterior pinnal plate. It has also lost the first intermediate spine, this being a continuation of the trend which started with the loss of the posterior pinnal plate. Judged solely on the shoulder-girdle, it would be possible to regard *Euthacanthus* as more closely related to *Parexus* and *Vernicomacanthus* than to any other genera. This conclusion, if accepted, would demand some rearrangement of the existing classification, as at present *Euthacanthus* (Euthacanthidae) is placed apart from the Climatiidae. However, these groups differ notably from each other in the structure of the head, and for this reason I conclude that the similarities between *Euthacanthus* on the one hand and *Vernicomacanthus* and *Parexus* on the other, are the result of parallel evolution.

If *Gyracanthus* has been correctly interpreted, it is uniquely specialised in the reduction of the dermal girdle to a second middle-posterior pinnal plate with a ventral lamina and low ascending lamina behind the paired prepectoral spine (no. 3). It seems clear that the gyracanthids are more closely related to climatiids than they are to euthacanthids, but there is not enough information on which to base a discussion of their relationships. I maintain, therefore, their rank as a separate family.

V. COMPARISON BETWEEN CLIMATIOIDS AND DIPLACANTHOIDS

Diplacanthoids differ from climatioids such as *Climatius* and *Erriwacanthus* in the absence of prepectoral spines, the total reduction of the lorical plates (see p. 194), the reduction of the pinnal series to the posterior plate, and the hypertrophy of the first intermediate spine. Too few diplacanthoids are known for the evolutionary tendencies to be firmly established, but it is assumed that the dermal shoulder-girdle of a primitive diplacanthoid resembled that of a primitive climatioid in the presence of anterior pinnal, middle pinnal and lorical plates, and prepectoral spines. If so, diplacanthoids have paralleled climatioids in the reduction of the exoskeleton, but the changes have taken a different form, leading to the retention of the posterior pinnal plate rather than its loss, and to the suppression of the more anterior elements rather than their retention in some modified form.

The retention of the posterior pinnal may be correlated with the hypertrophy of the first intermediate spine, and not with the anchorage of the pectoral spine or the structure of the scapulocoracoid. It may be noted, however, that the posterior pinnal differs from that of climatioids in not extending mesially to the first intermediate spine.

The high scapular blade and strongly ribbed fin-spines are further characters in which climatioids and diplacanthoids resemble each other. Diplacanthoids are more advanced in the coracoid region, as they possess a separate procoracoid; and in this they have paralleled acanthodiforms and ischnacanthiforms. It is possible that there is a correlation in diplacanthoids between the possession of a procoracoid and the early loss of the anterior lorical and pinnal plates, particularly as there may be a phylogenetic (and ontogenetic?) connexion between the development of these plates and the coracoid process in primitive climatiiforms. I have suggested above that the dermal element attached to the procoracoid in diplacanthoids is a new structure that cannot be homologised with the pinnal or lorical plates.

This study of the shoulder-girdle strongly supports the current classification of climatiiforms into climatioids and diplacanthoids; this reflects a basic dichotomy of the group. However, Ørvig (1967 : 139), in an unexplained statement, has written that there appears to be more resemblance between diplacanthoids and *Erriwacanthus* (and *Climatius*) than between these genera and euthacanthids. He may be alluding to primitive characters.

VI. EVOLUTIONARY TENDENCIES IN ACANTHODIFORMS

The evolutionary tendencies in this group can be derived from the sequence *Mesacanthus* (Lower–Middle Devonian) – *Cheiracanthus* (Middle Devonian) – *Acanthodes* (Carboniferous–Lower Permian), assuming that the series arises in an hypothetical first term with a climatioid-like scapulocoracoid. They include:

(1) An increase in the ossification of the coracoid region.

(2) The division of the scapulocoracoid with the development of a separate procoracoid.

(3) The development of a moveable joint between the procoracoid and the scapulocoracoid.

(4) The development of a mobile pectoral spine.

These changes may be accompanied by the enlargement of the margo radialis; and the increased ossification of the coracoid region may indicate the development of more powerful fin muscles. It is unfortunate that *Mesacanthus* is poorly known, but the above statements are sustained by the conjecture that primitive acanthodiforms had fin articulation and fin muscle insertion areas of similar extent to those of the climatioid *Sabrinacanthus*. The coracoid process of climatioids can be homologised readily with the procoracoid of *Cheiracanthus* and *Acanthodes*. The joint between the procoracoid and scapulocoracoid corresponds in position with the posterior endochondral lamina of *Sabrinacanthus*.

The shoulder-girdle is still not well known in a sufficiently wide range of acanthodiforms for further conclusions to be drawn. But what is known appears to support the view that the division of this group into the Mesacanthidae, Cheiracanthidae and Acanthodidae results in a horizontal (grade) rather than a vertical (clade) classification (Miles 1966 : 174).

VII. THE INTERRELATIONSHIPS OF THE ACANTHODIAN ORDERS

It is regrettable that this study has not thrown more light on the problem of the interrelationships of the acanthodiforms, ischnacanthiforms and climatiiforms. The climatiiforms are the most distinct group, because of the presence of a dermal shoulder-girdle and prepectoral spines. It is likely that the extensive development of these structures is primitive for climatiiforms, but there is no good evidence that they are primitive for acanthodians as a whole. In particular there is no indication of their recent loss in the most primitive acanthodiforms and ischnacanthiforms. Acanthodiforms and ischnacanthiforms may thus resemble each other in the lack of these structures because (1) this is a shared primitive character, or (2) they have independently lost these structures, thus paralleling climatiiforms in the general reduction of the exoskeletal shoulder-girdle. In neither case would the explanation indicate a close relationship between the two groups. The third possibility, that the exoskeleton was lost in the common ancestors of these groups, cannot be demonstrated with the materials at hand. Some further, incomplete evidence is provided by the internal shoulder-girdle. A procoracoid is found in acanthodiforms, ischnacanthiforms and diplacanthoids, and although independently acquired it shows more resemblance in the first two groups than between either of these groups and the diplacanthoids. This may indicate the relative genetic affinity of these groups.

In view of the almost total lack of evidence bearing on the interrelationships of acanthodian orders, it is necessary to propose a tentative hypothesis that can be tested as more information becomes available on acanthodian structure. I suggest that the acanthodiforms and ischnacanthiforms shared a common ancestor more recently than either group shared a common ancestor with the climatiiforms. This hypothesis does not warrant any changes in the formal classification of acanthodians.

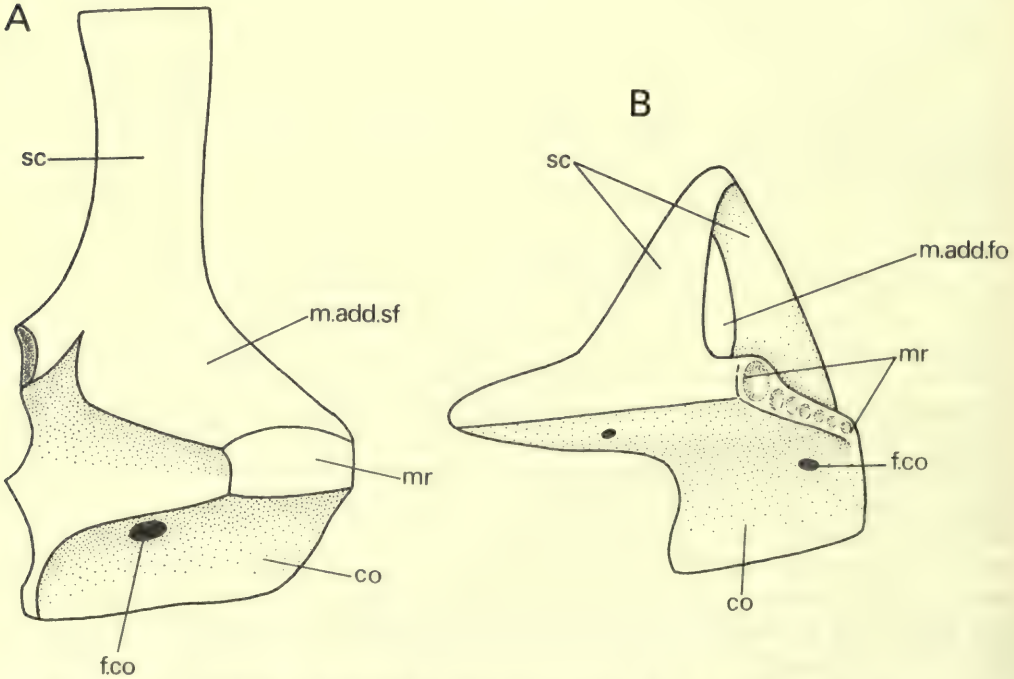
If this hypothesis is correct, the common possession of teeth by climatiiforms and ischnacanthiforms is probably a primitive character without phylogenetic significance. It is interesting to note, therefore, similarities in the dentitions of Upper Silurian species of these groups (Ørvig 1967), which suggest divergence from a primitive acanthodian type.

VIII. COMPARISONS WITH OTHER GROUPS OF FISHES

Scapulocoracoid

Romer (1924) has shown that the scapulocoracoid in primitive Recent osteichthyans (*Neoceratodus*, *Polypterus*, *Scaphirhynchus*, *Lepisosteus*, *Amia*) is of the same general type as in primitive tetrapods; and Andrews & Westoll (1970) have demonstrated that the scapulocoracoid of the rhipidistian *Eusthenopteron* is also of this type. These genera exhibit a coracoid plate, supraglenoid buttress (or mesocoracoid), supraglenoid and coracoid foramina, and areas for the origin of the dorsal and ventral fin muscles. The Recent genera also have distinct middle and scapular regions of the girdle. It is clear from the terminology used in the descriptions in this paper that *Acanthodes* closely matches this general type, having all the above characters, although it is specialised in the presence of a pectoral spine groove, procoracoid process, separate procoracoid and pectoral fossa (not found in climatioids). However, the significance of this general agreement is not clear, because the scapulocoracoid of chondrichthyans appears to be built on the same basic plan, with scapular and coracoid regions, and supraglenoid and coracoid foramina (Goodrich 1930: 164–165; Daniel 1934 : 79–81). It seems probable that Romer's work has established the basic type of gnathostome scapulocoracoid (but cf. placoderms, p. 205).

Despite the above conclusions, it seems worth while drawing attention to the close correspondence in structure between *Acanthodes* and palaeoniscoids such as *Pteronisculus* and *Moythomasia* (Nielsen 1942; Jessen 1968) and sturgeons (Sewertzoff 1926). The hollowed coracoid plate for the origin of the ventral muscles, and the broad, horizontal margo radialis are striking similarities (Text-fig. 43). The most important difference, apart from those involving the specialisations of *Acanthodes* listed above, is the absence of a dorsal muscle fossa in the base of the scapula in *Acanthodes*. However, if we now turn to the only other acanthodians in which the scapulocoracoid is well known, the climatioids *Sabrinacanthus* and *Ptomacanthus*, these similarities largely disappear, despite the absence in these genera of the specialisations associated with the mobile pectoral spine in *Acanthodes*. *Ptomacanthus* is close to elasmobranchs in the structure of the scapulocoracoid, particularly in the high, broad scapular blade, long coracoid process and apparent connexion with its fellow in the middle line. Xenacanth sharks, however, are said



TEXT-FIG. 43. Comparison between the scapulocoracoid of A, *Acanthodes* (see Text-fig. 19) and B, a palaeoniscoid, *Moythomasia* cf. *striata*, Upper Devonian. B, after Jessen 1968, Text-fig. 7A. Both figures in approximately lateral view from left side.

to have unconnected scapulocoracoids, each with an 'infra-coracoidal' (and suprascapular) element (Goodrich 1930 : 164), and thus resemble *Acanthodes* rather than climatioids. A long coracoid process may be primitive for both acanthodians and chondrichthyans, and is also found in placoderms (Stensiö 1944, 1959). It is the site of origin of important hypobranchial muscles, and its reduction in acanthodiforms is the result of changes with a clear functional explanation (p. 202). The well developed scapular blade of *Ptomacanthus* is a character shared to some extent by all acanthodians, and among bony fishes by sturgeons (Severtzoff 1926, Text-fig. 10, 14; Goodrich 1930, Text-fig. 172; Jessen 1968, Text-fig. 7C, D). The significance of this blade in acanthodians and chondrichthyans lies in the absence of lateral, exoskeletal shoulder-girdle plates (Miles 1965 : 244); it serves to anchor the girdle in the body muscles and is a site for the origin of the superficial trapezius muscles. The extent of the scapular blade is, therefore, of doubtful phylogenetic significance, and this conclusion is reinforced by placoderms. In these elasmobranchiomorphs an exoskeletal 'shoulder-girdle' in the form of the trunk-shield is normally well developed, and the scapulocoracoid is a low structure without a scapular blade. The great differences between the scapulocoracoids of acanthodians and placoderms may be emphasised, because these groups have sometimes been classed together (Moy-Thomas 1939). The long, low scapulocoracoid of arthrodires appears basically to be crossed by a long series of diazonal nerves, each accompanied by a segmental artery and vein, and is difficult to compare with the basic adult gnathostome scapulocoracoid discussed above. Stensiö (1959) has had some success in interpreting it by comparison with the scapulocoracoids of shark embryos.

It may be concluded that the scapulocoracoid of acanthodians does not point decisively to either elasmobranch or teleostome relationships for this group, although it does corroborate the conclusion that they are not closely related to placoderms. The scapulocoracoid is probably close to the basic gnathostome type. It is unfortunate that the margo radialis is not more widely known, for the horizontal crest of *Acanthodes* is decidedly osteichthyan-like and there is some evidence that it has a similar form in *Sabrinacanthus*. In contrast, the glenoid of elasmobranchs seems normally to take the form of a knob or vertical depression in Recent species (Goodrich 1930; Daniel 1934; Smith 1937), and it may be like this or as an ill-defined lateral area (if the basal axis is in the body wall) in fossil forms (Schaeffer 1967, Text-fig. 1–6). Whether this similarity between acanthodians and early osteichthyans is dictated by function or propinquity of descent cannot yet be decided.

Dermal skeleton

Although scales may coat the outside of the scapulocoracoid, or fuse into a small plate as in diplacanthoids, there are no true, lateral exoskeletal shoulder-girdle bones in acanthodians. There are, however, ventral bones in climatiiforms, and it is possible to compare some of them with the bones of the osteichthyan girdle (Jarvik 1944) by virtue of their relationship to the pectoral fin and hind wall of the gill-chamber. Thus, using the hypothetical primitive climatioid pattern, the posterior pinnal may be compared with the ventral lamina of the cleithrum, the middle pinnals with the clavicle and the posterior lorical with the interclavicle. Yet it is obvious that the correspondence is not exact, and the comparison takes no account of the anterior lorical and pinnal plates. Other comparisons can be made taking these plates into account, with, for example, the boundary between the cleithral and clavicular regions drawn between the first and second middle pinnal plates, and the anterior lorical homologised with the interclavicle. But because of the imprecise nature of these comparisons, I am inclined to regard the ventral shoulder plates of acanthodians and osteichthyans as independently acquired structures, and the similarities between them as fortuitous. In favour of this view is the conclusion that most of the plates (not the posterior lorical) in climatiiforms are related to a prepectoral or intermediate spine. Such spines are not found in osteichthyans. Nevertheless, the independent development of similar shoulder-girdle plates in acanthodians and osteichthyans might be due to the inheritance of a common genetic potential.

A similar comparison can be made between climatiiform plates and the ventral plates of the trunk-shield in placoderms. But this comparison is far fetched and even less convincing than the comparison with osteichthyans. It may be true that the pectoral spine of placoderms is formed primitively around a lateral prepectoral process of the scapulocoracoid, like the fin-spine of a primitive acanthodian. Nevertheless, I believe it is entirely coincidental that the posterior pinnal of *Diplacanthus* attaches to the pectoral spine in the same way that the anterior ventrolateral plate clasps the spinal plate in placoderms (cf. Watson 1937 : 132).

Westoll (1967 : 97) has suggested that 'the scapular blade of elasmobranchs and of tetrapods may be a development from dermal shoulder-girdle elements', by the operation of delamination during phylogeny. There is no evidence that this is the explanation of the prominent scapular blade in primitive acanthodians, and if one concludes that acanthodians have never had an osteichthyan type of dermal shoulder girdle or placoderm-like trunk-shield, this explanation cannot be applied. The internal and external shoulder-girdles of fishes probably had separate origins (Jarvik 1965 : 152). It is not possible to say which arose first in a general statement framed to cover all groups, but in placoderms and osteichythans it is normally the dermal girdle and in acanthodians and chondrichthyans the endoskeletal girdle which is prominently developed.

Pectoral fin

In view of the often repeated, incorrect statement that the intermediate spines of acanthodians carried fins, it is necessary to stress that none of the prepectoral-intermediate spines in climatiiforms was equipped with a web, and that the pectoral fin was the only fin that articulated with the girdle. The pelvic, intermediate and prepectoral spines form a single, paired series in a ventrolateral line of potential fin development along the body (Westoll 1958; 'ventrolateral crest', Jarvik 1965). From Text-figs 25, 27, and the restorations of Watson (1937, Text-figs 2B, 4) and

Ørvig (1967, Text-fig. 2), it is obvious that the pectoral fin-spine lies outside this series. Nevertheless it probably arose in the same line as the other spines, and has been secondarily displaced laterally together with the base of the fin, either for hydrodynamic reasons or because of the size of the web. I cannot accept an alternative explanation which supposes that there were laterally two lines of potential fin development, although Ørvig (1961 : 517, footnote) has suggested that there may be structures representing two or more pairs of lateral 'potential fin-folds' in certain agnathans.

The skeleton of the pectoral fin is only well known in *Acanthodes bronni*, in which I have interpreted it as actinopterygian-like (p. 153), in contrast to Watson (1937) who regarded it as forming a tribasal structure of elasmobranch type. The 'ceratotrichia' and lepidotrichia-like rows of scales in acanthodians have been discussed elsewhere (Miles 1970 : 358); they permit no phylogenetic conclusions to be drawn. The presence of fin scales in some Lower Devonian climatioids indicates that the pectoral fin had a large, well-developed web and a short base, in the earliest articulated species. It now seems clear that the fins were more than mere 'thick, fleshy fin-folds' (Westoll 1945, 1958), and this is supported by the presence of an *Acanthodes* type of internal skeleton in the Lower Devonian species *Ischnacanthus gracilis*.

Clear trends of change can be seen in the pectoral spines (Westoll 1945, 1958). An instructive morphological series comprises a climatiid (e.g. *Ptomacanthus*) – *Mesacanthus* – *Cheiracanthus* – *Acanthodes*. These forms show a progressive change from a short, coarsely ornamented spine firmly fixed to the scapulocoracoid, to a long, slender, smooth spine moveably articulated and capable of erection. These changes are possibly correlated with the reduction of the intermediate spines. It is not possible to say definitely whether they are paralleled in ischnacanthiforms and climatioids, but this is likely, and if they are they explain the reduction of the exoskeletal girdle in climatioids.

The pectoral spines of advanced acanthodiforms invite comparisons with the analogous pectoral spines of sturgeons and catfishes, which are formed from hypertrophied lepidotrichia. Jarvik (1965 : 151, Text-figs 5E, F, 10D) has touched on this subject, and has figured a young *Acipenser ruthenus* which clearly shows the position of the pectoral spine lateral to the ventrolateral crest, like the pectoral spine of acanthodians. It is, perhaps, remarkable that analogous spines have not been produced in chondrichthyans, despite the presence of scales on the fin. This might have a functional explanation; it may reflect differences in the inherited evolutionary potential of chondrichthyans and teleostomes; or the difference may be purely aleatory.

In addition to their hydrodynamic significance, the pectoral spines of catfishes have a protective function (Alexander 1965), and probably this is also true of acanthodians. A fish with erect spines is more difficult for a predator to swallow whole, although for the spines to be effective they must also be firmly held in position so that they are not depressed by the predator's jaws. Whilst it is clear that the pectoral spines could be erected in *Acanthodes*, there is no indication of a locking mechanism (cf. catfishes; Alexander 1965). This may, therefore, have been muscular, relying on the same muscles that were used to erect and depress the spine (p. 155). It is possible that the ventral dermal plates of climatiiforms were initially evolved to give a firm mounting for the pectoral and associated spines. However, this explanation makes it difficult to understand the early reduction of the posterior pinnal plate and freeing of the pectoral and first intermediate spines in climatioids, unless the pectoral spine became mobile and was provided with a muscular locking mechanism. The fixedness of the pectoral spines of primitive climatiiforms may be correlated with their short length, but if this is so, it suggests that at least the long pectoral spines of gyracanthids were mobile. In acanthodiforms the dorsal, pelvic and intermediate spines are reduced as the pectorals become elongated and more mobile, and therefore more efficient defences, and these changes may have been paralleled to some extent in the gyracanthids.

This study has produced no compelling evidence on the relationships of acanthodians to elasmobranchs and osteichthyans, but it confirms that they are not closely related to placoderms and does not deny the osteichthyan affinities suggested by the study of cranial structures. The skeleton of the pectoral fin and the form of the margo radialis are consistent with this view. I hold, therefore, to my earlier conclusion that acanthodians are a line of teleostomes collateral with the osteichthyans.

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X. ABBREVIATIONS USED IN FIGURES

ALo	anterior lorical plate
AM1,2Pl	anterior – first middle – second middle pinnal plate
AM2Pl	anterior – second middle pinnal plate
APl	anterior pinnal plate
CPl	copinnal plate
Ha	anterior elements in dorsal region of hyoid gill-cover
Hp	posterior elements in dorsal region of hyoid gill-cover
Lo	lorical plate
M1Pl	first middle pinnal plate
M2Pl	second middle pinnal plate
M1,2PPl	first middle – second middle – posterior pinnal plate
Pl.la.a	anterior endochondral lamina
Pl.la.m	middle endochondral lamina
Pl.la.p	posterior endochondral lamina
PLo	posterior lorical plate
PPl	posterior pinnal plate
V3	notch for ramus mandibularis trigemini
Z1–Z4	scale zones of caudal fin (explained in text)
Ia–IVa	anterior dermal elements in gill-covers 1 to 4
Ip–IVp	posterior dermal elements in gill-covers 1 to 4
Ivt	ventral tesserae of gill-cover 1
ad.sp	anterior dorsal spine
al	ascending lamina
a.sp	anal spine
bpl	basal plate of tooth
br	branchiostegal ray
br.a	anterior exoskeletal elements of gill-arches
br.p	posterior exoskeletal elements of gill-arches
cart(mr)	cartilaginous region around margo radialis
cav.p.sp	cavity of pectoral spine
cav.sp	cavity of prepectoral-intermediate spine
ch.edg	bevelled edge of pinnal plate
cmo	circumorbital plates
co	coracoid
cp	tooth cusp
cr.epq	extrapalatoquadrate ridge
dc	dorsal sensory commissure
derm.l	lateral dermal plate
derm.v	ventral dermal plate
dg.b	dentigerous bone
dmf	dorsal muscle fossa
dnvc	dorsal neurovascular canals
dp.pe	pericardial depression
end	endolymphatic duct
f.add	adductor fossa
f.co	coracoid foramen
ff	foramina on inner face of scapula
fo.p	pectoral fossa
fo.sbsc	subscapular fossa
gcl	gill-clefts
gl.pr	glenoid process
hgf	hyoid gill-flap
inf.ot	otic branch of infraorbital sensory-line
isp 1–6	intermediate spines 1 to 6
jut	juglar tesserae
la.l	lateral lamina of pinnal plate
la.pbr	postbranchial lamina of pinnal plate
las	labial surface of tooth
la.v	ventral lamina of procoracoid
lj.t	lower jaw teeth
ll	main lateral-line
m.add.fo	fossa for adductor muscles
m.add.sf	surface for origin of adductor muscles
mk	meckelian cartilage
mk.a	mentomandibular
mk.p	articular
mr	margo radialis
na	external nasal opening
nt	navicular tesserae
pbpr	prebranchial projection
p.f	posterior flange of scapula
pfc	‘profundus’ sensory-line
p.gr	pectoral groove (for pectoral spine)
poc	preopercular sensory-line
popr	postorbital projection
ppsp 1–3	paired prepectoral spines 1 to 3
ppsp.m	median prepectoral spine
pq	palatoquadrate
pr.art	articular process
pr.preart	prearticular process
pr.co	coracoid process
proco	procoracoid
pr.pregl	preglenoid process
pr.d	dorsal posterior process of procoracoid
pr.dl	dorsal process of procoracoid

pr.proco	procoracoid process of scapulocoracoid
pr.v	ventral posterior process of procoracoid
p.sp	pectoral spine
p.sp.cf	contact face for pectoral spine
psp.f	fossa for pectoral spine
pv.f	pelvic fin
pv.sp	pelvic spine
ra	radial
rdg	ridge down scapula
rdg.a	anterior ridge of posterior pinnal plate
rdg.p	posterior ridge of posterior pinnal plate
rdg.pcav	ridge posterior to opening of prepectoral spine
rdg.Pl	ridge around mesial region of posterior pinnal plate
rdg.ppsp	ridges on leading face of prepectoral spine
sc	scapula
scco	scapulocoracoid
sc.oa	scapular overlap area
scp	side cusp
shg	shoulder-girdle
sml	supramaxillary sensory-line
soc	supraorbital sensory-line
sqt	squamosal tesserae
ssc	suprascapula
t	teeth
tgu	gular tesserae
tt	tectal tesserae
uj.t	upper jaw teeth
vl	ventral lamina
vmf	ventral muscle fossa
vnvc	ventral neurovascular canals
vll	ventral lateral-line

R. S. MILES, D.SC.
Department of Palaeontology,
BRITISH MUSEUM (NATURAL HISTORY)
Cromwell Road
London SW7 5BD

PLATE 1

Vernicomacanthus waynensis gen. et sp. nov.

FIG. 1. Cast of holotype, BM P.24938a. Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

Ptomacanthus anglicus gen. et sp. nov.

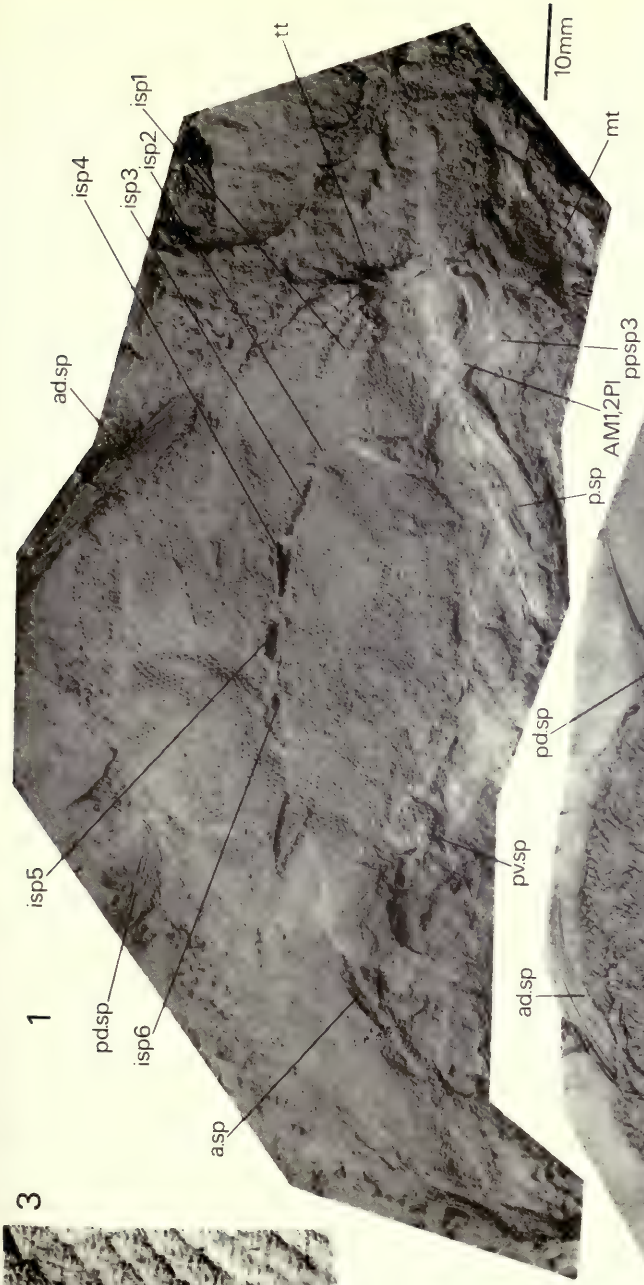
FIG. 2. Cast of holotype, BM P.19999. Horizon and locality as for fig. 1.

Vernicomacanthus waynensis gen. et sp. nov.

FIG. 3. Cast of holotype, BM P.24938a. Detail of flank scales. Horizon and locality as for fig. 1.

Photos: T. W. Parmenter.

1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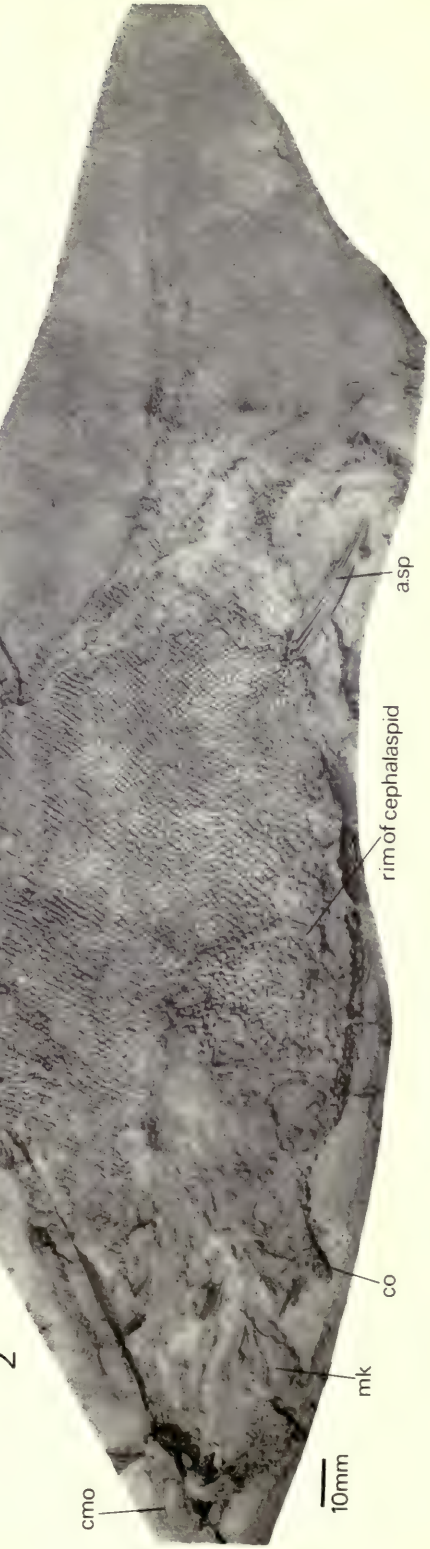
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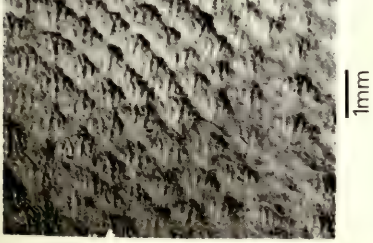
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PLATE 2

Climatius reticulatus Agassiz

Head of BM P.1343. Use Text-fig. 5 as key-diagram. Arbuthnott Group, Dundee Formation, Lower Old Red Sandstone, Turin Hill, Angus, Scotland.

Photo: Tordis Junker.

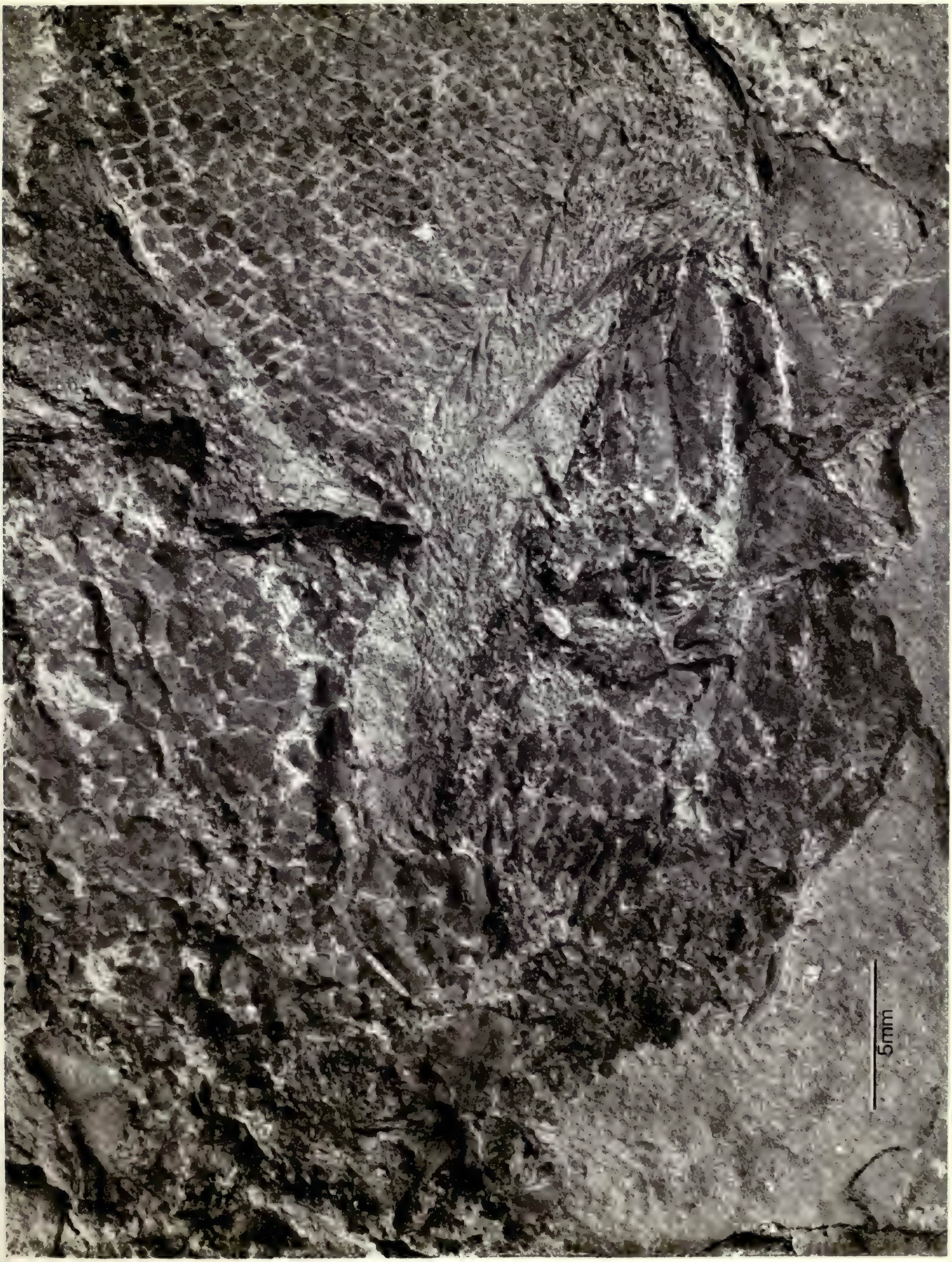

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PLATE 3

Climatius reticulatus Agassiz

Right jaw cartilages, teeth and part of left shoulder-girdle. GSM 49785 Arbuthnott Group, Dundee Formation, Lower and Red Sandstone, Turin Hill, Angus, Scotland. In alcohol.

Photo: T. W. Parmenter.

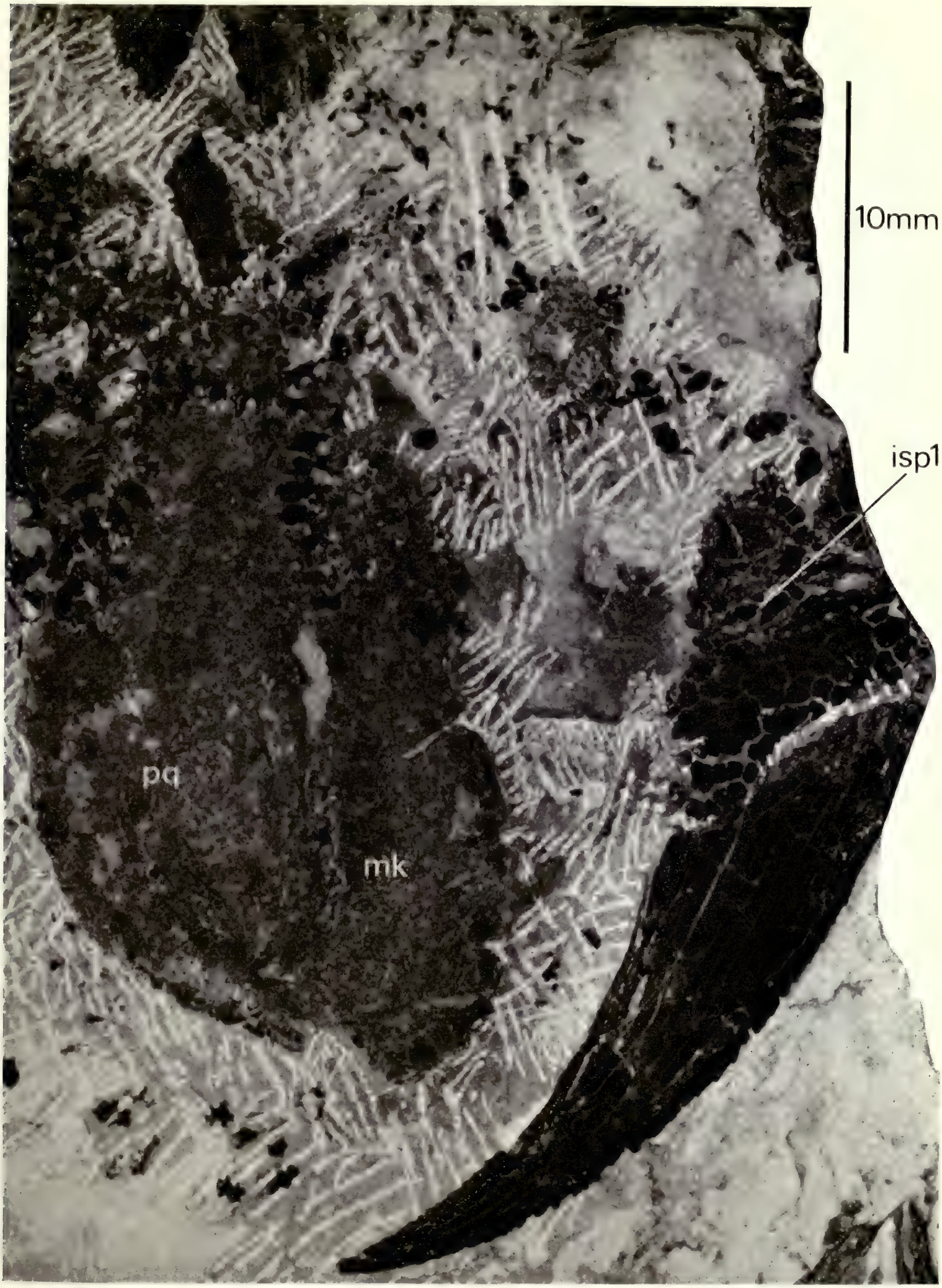
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PLATE 4

Ptomacanthus anglicus gen. et sp. nov.

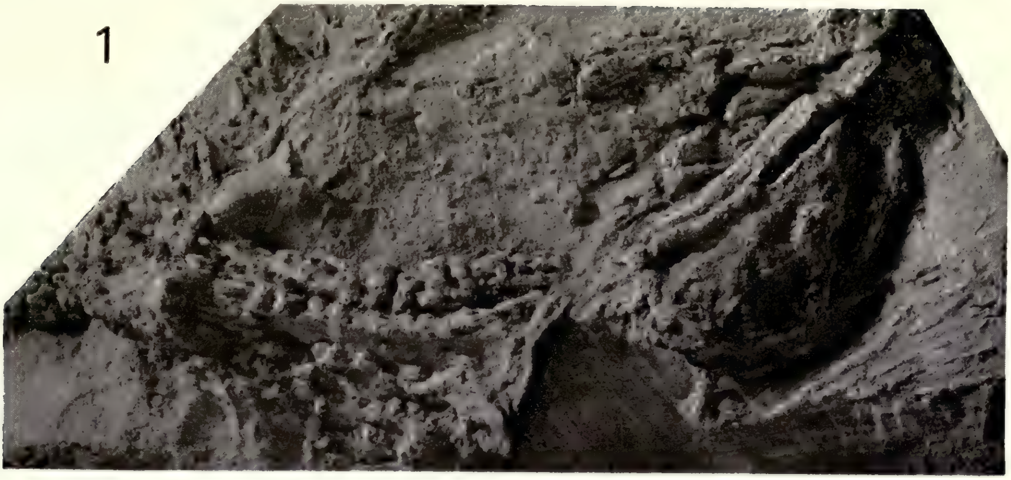
Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

FIG. 1. Cast of holotype, BM P.19999. Detail of palatoquadrate and meckelian cartilage. Use Text-fig. 12 as key-diagram.

FIG. 2. Cast of BM P.20003. Detail of shoulder-girdle. Use Text-fig. 4 as key-diagram.

Photos: T. W. Parmenter.

1



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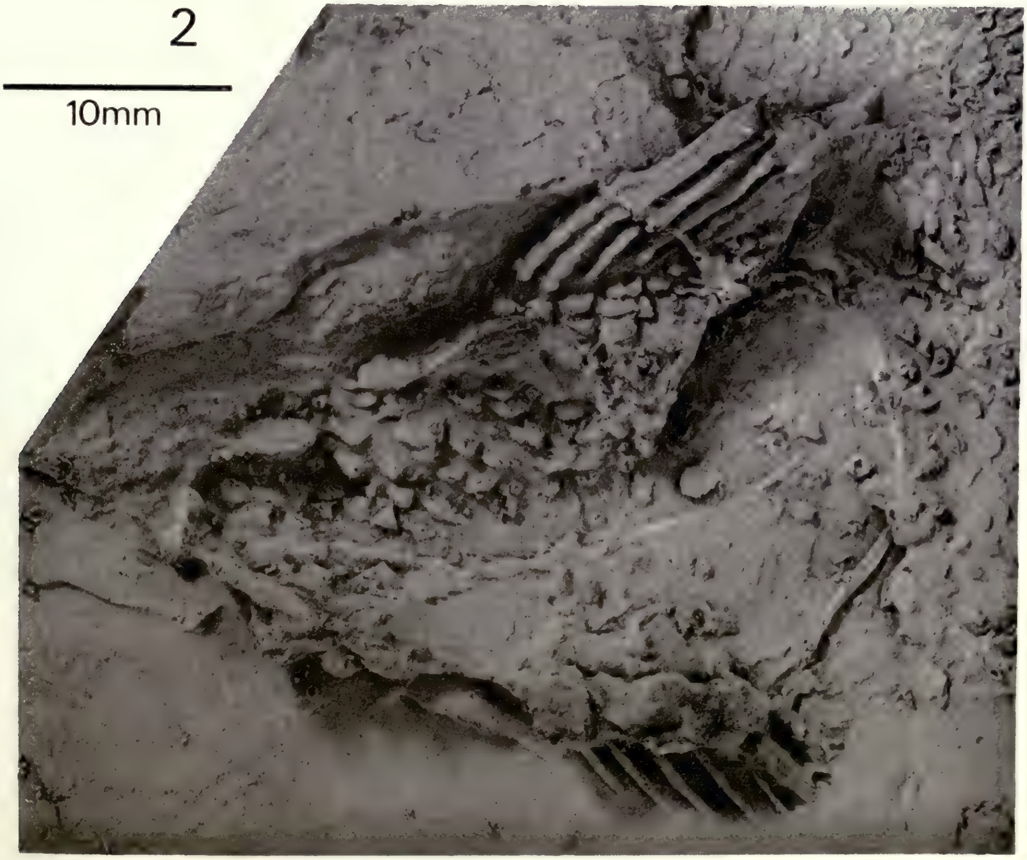

PLATE 5

Ptomacanthus anglicus gen. et sp. nov.

Flattened head in dorsal view. Cast of BM P.24919b. Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

Photo: T. W. Parmenter.

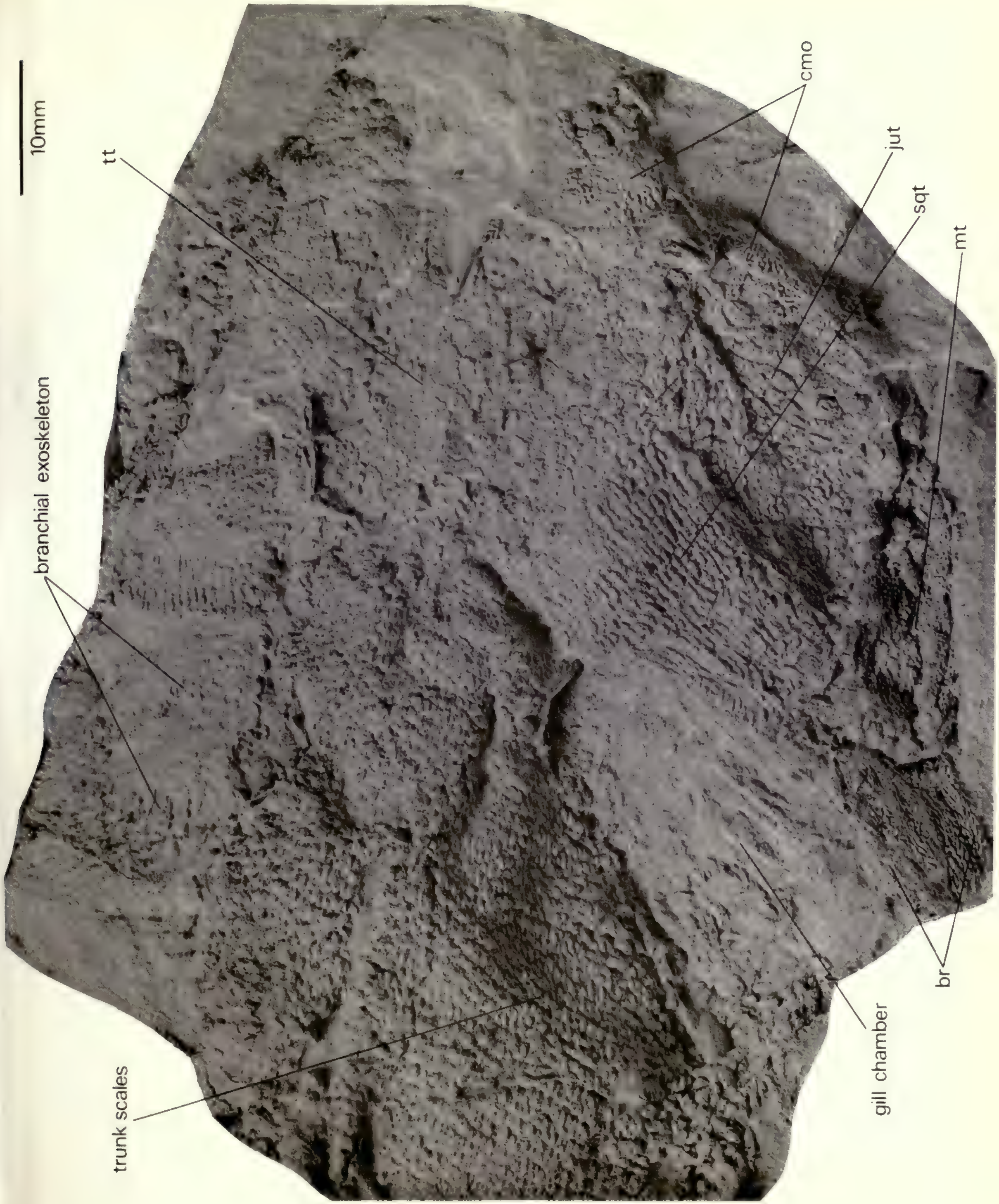
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PLATE 6

Ptomacanthus anglicus gen. et sp. nov.

Flattened head in ventral view with upper dentition *in situ*. Cast of BM P.24919a. Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

Photo: T. W. Parmenter.

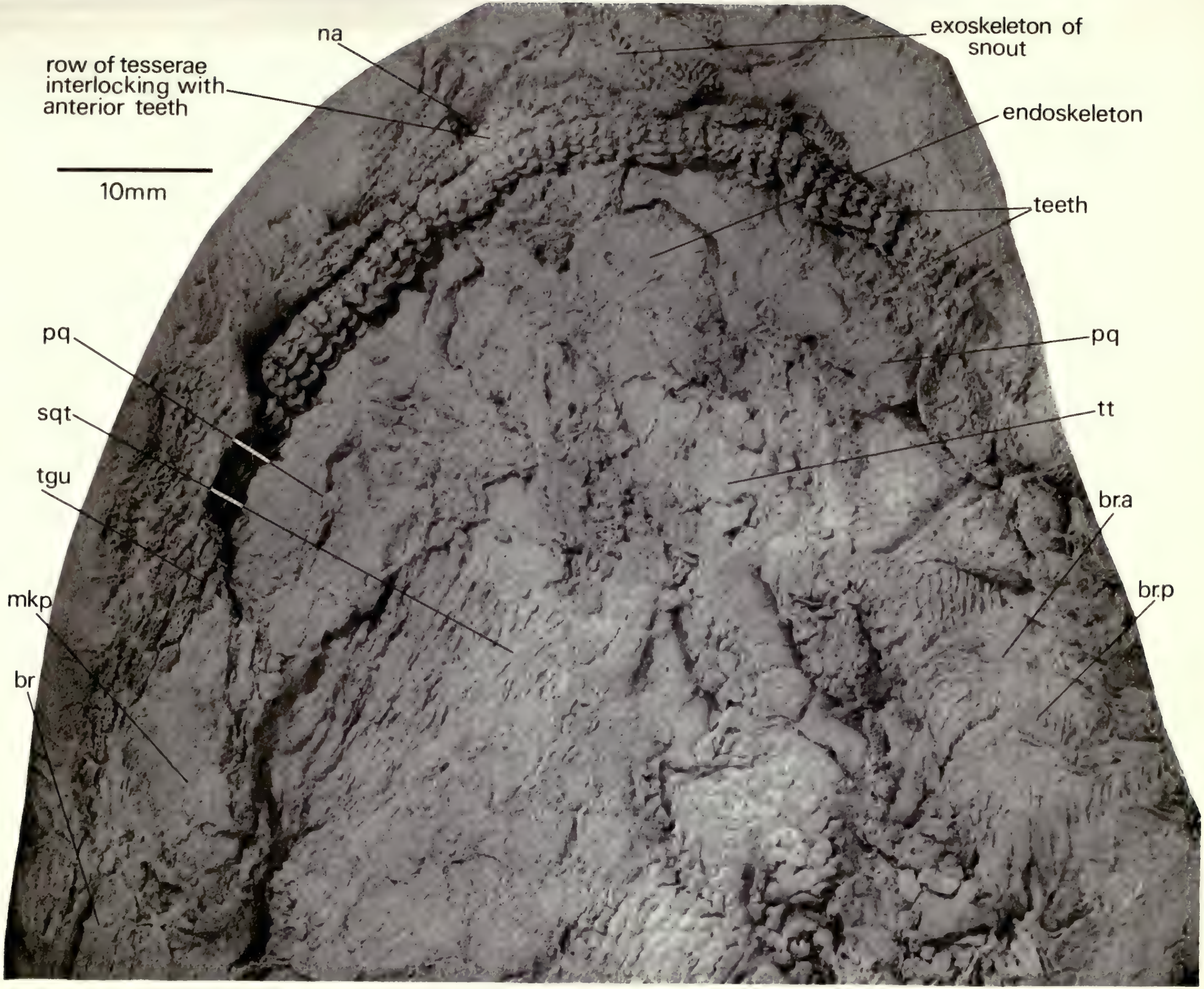
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PLATE 7

Vernicomacanthus gen. nov. ***uncinatus*** (Powrie)

Skull-roof, right cheek and shoulder-girdle in dorsal view. RSM Kinnaird collection 82. Arbuthnott Group, Dundee Formation, Lower Old Red Sandstone, Turin Hill, Angus, Scotland.

Photo: R. C. M. Thomson.

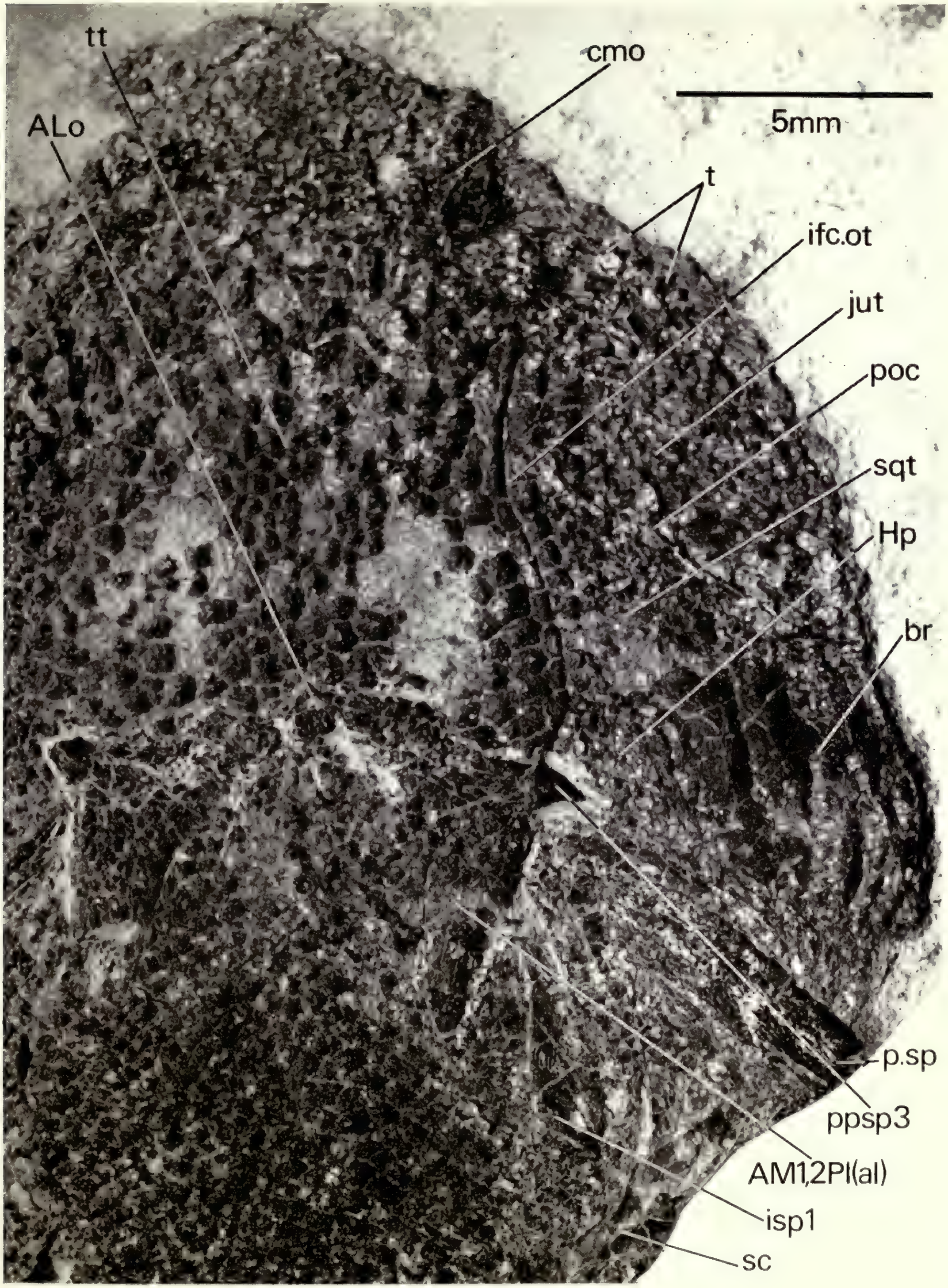
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PLATE 8

Vernicomacanthus waynensis gen. et sp. nov.

Cast of holotype, BM P.24938b. Counterpart of specimen in Pl. 1, fig. 1. Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

Photo: T. W. Parmenter.

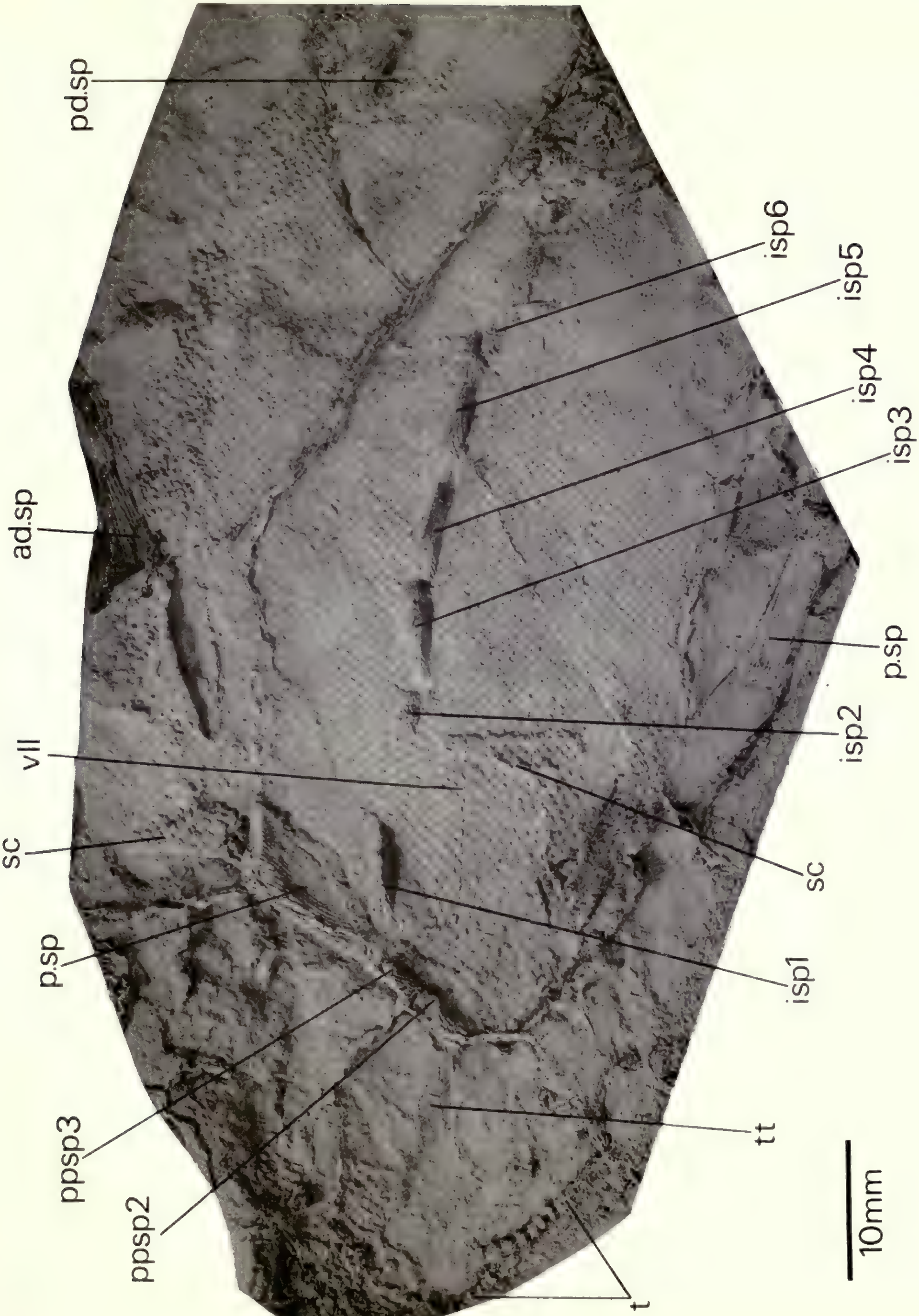
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PLATE 9

Vernicomacanthus waynensis gen. et sp. nov.

Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

FIG. 1. Cast of BM P.52441a. Detail of ventral surface in pelvic region.

FIG. 2. Cast of holotype, BM P.24938b. Detail of head and shoulder-girdle from same cast as in Pl. 8.

Photos: T. W. Parmenter.

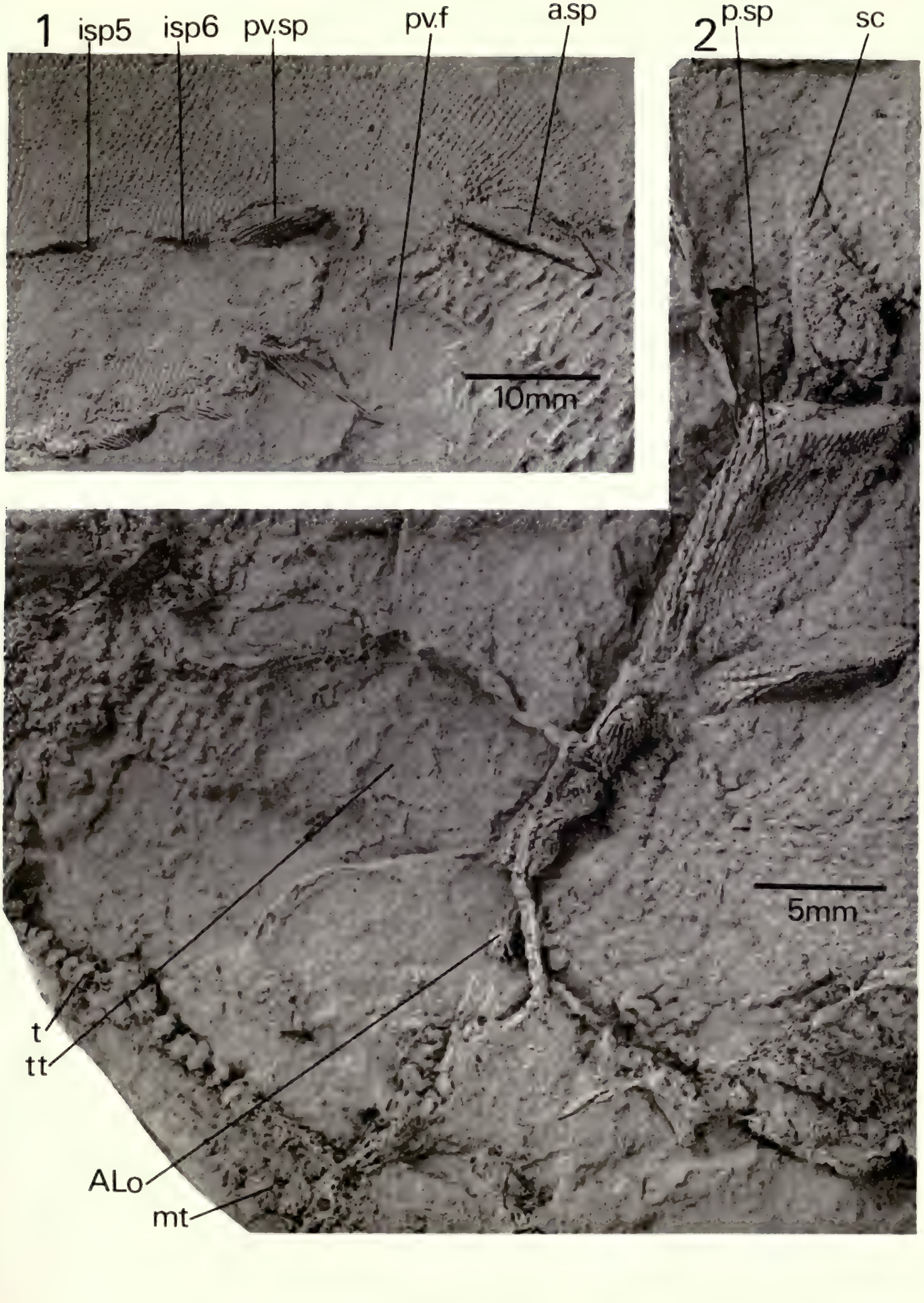
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PLATE 10

Vernicomacanthus waynensis gen. et sp. nov.

Cast of BM P.52441b. Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

Photo: T. W. Parmenter.

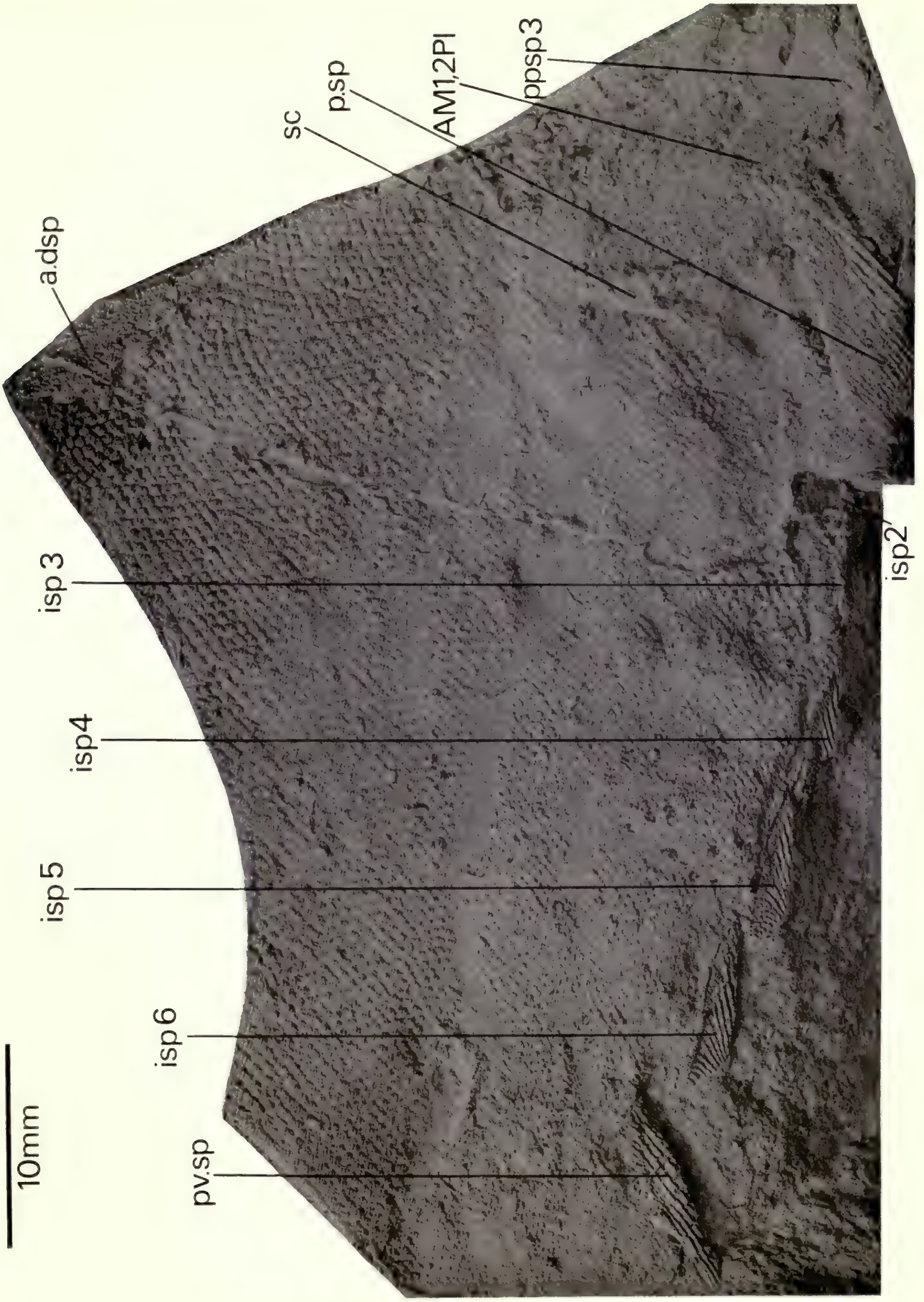

a.dsp
sc
p.sp
AM1,2PI
ppsp3
isp 3
isp2
isp4
isp 5
isp6
pv.sp
10mm

PLATE 11

Uraniacanthus spinosus gen. et sp. nov.

Cast of holotype, BM P.16609. Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

Photo: T. W. Parmenter.

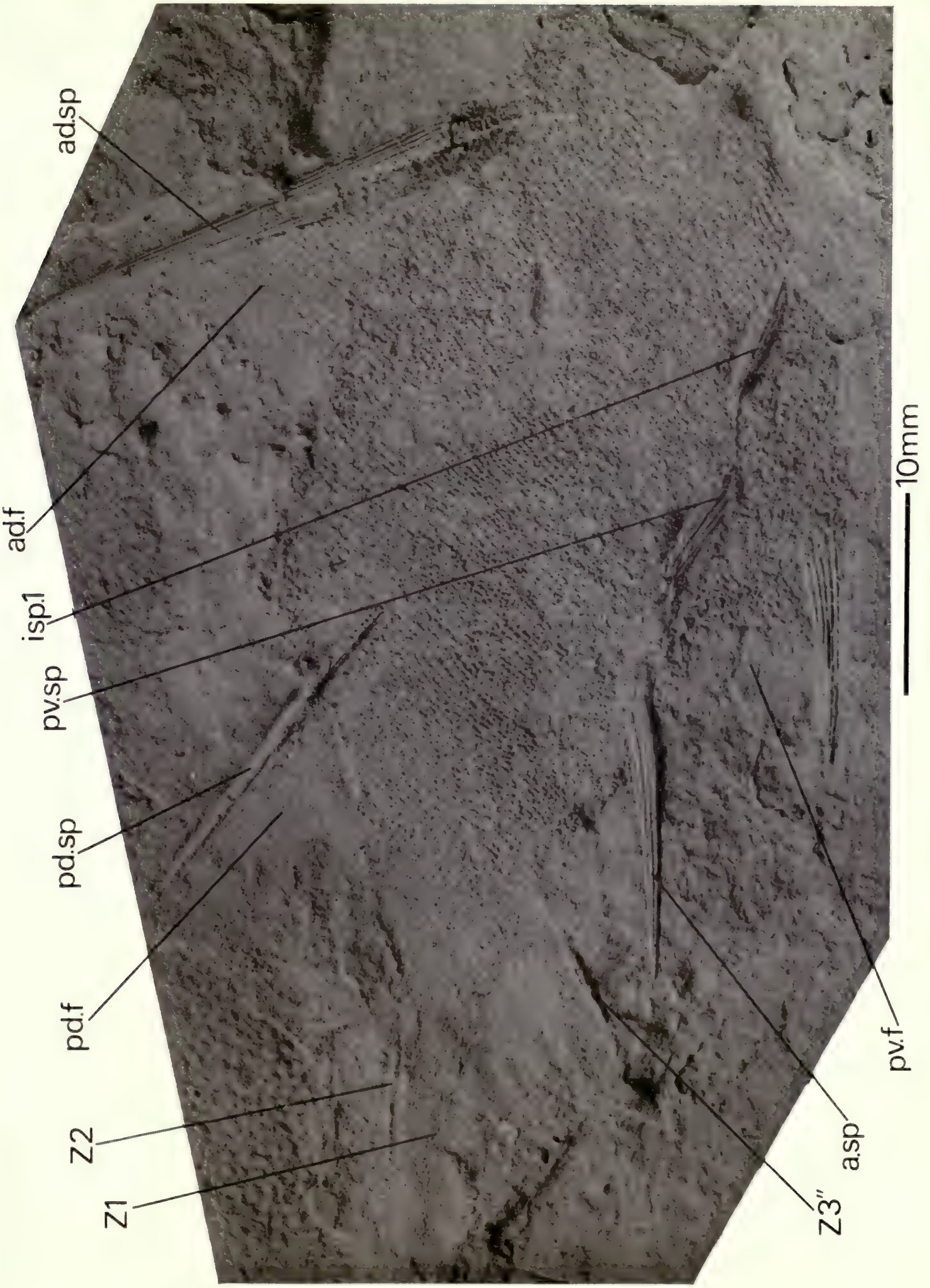

ad.sp
ad.f
isp.1
pv.sp
pd.sp
pd.f
Z2
Z1
Z3''
a.sp
pv.f
10mm

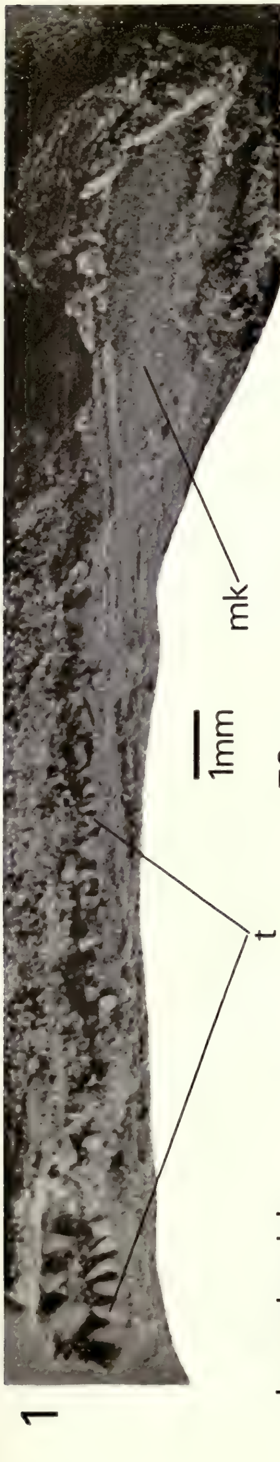
PLATE 12

Uraniacanthus spinosus gen. et sp. nov.

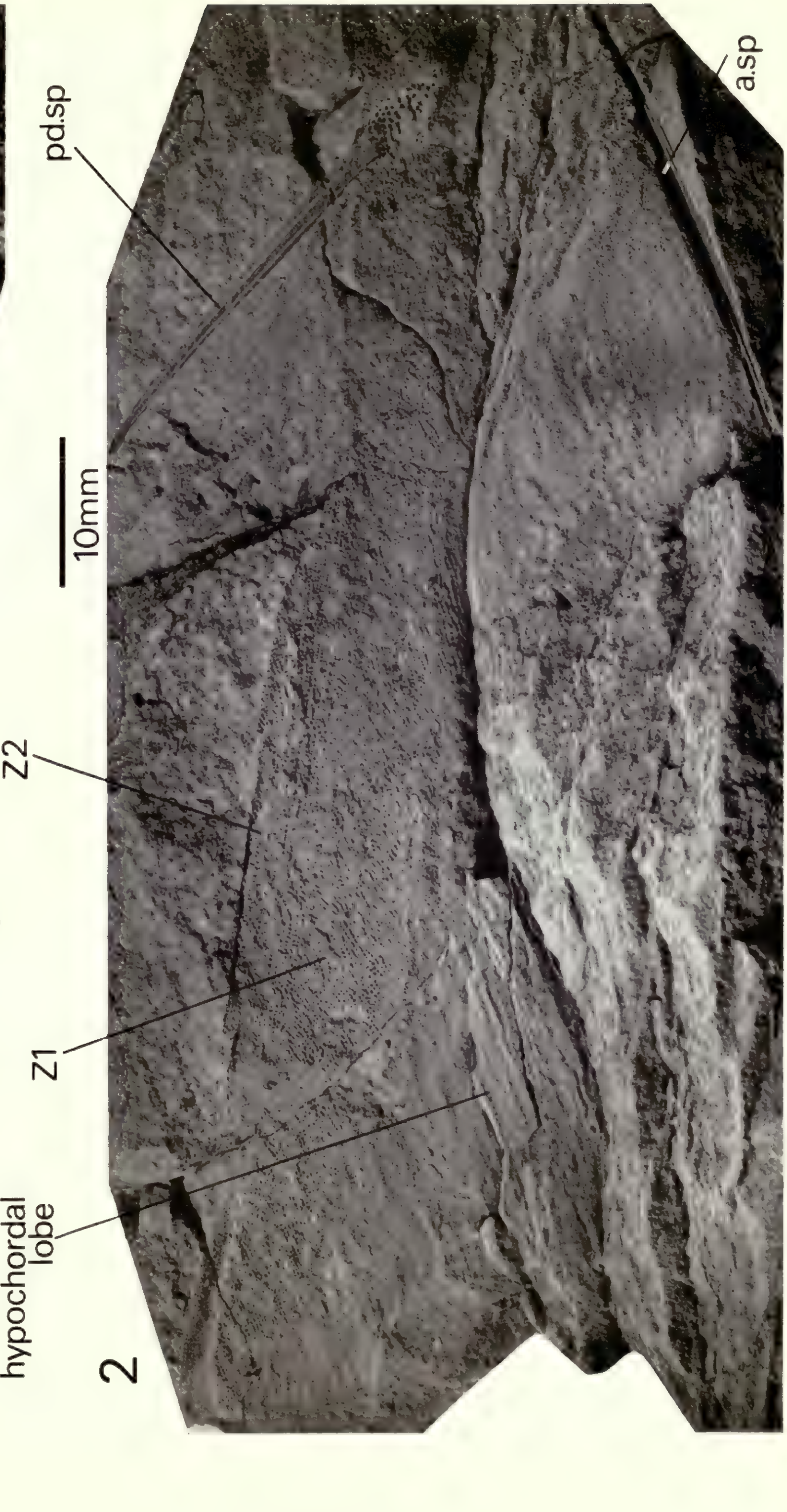
Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Newton, Herefordshire, England.

FIG. 1. Cast of BM P.53032. Incomplete jaws and teeth. Photo: Dr R. P. S. Jefferies.

FIG. 2. BM P.20001. Posterior part of body. Photo: T. W. Parmenter.



1


pd.sp
a.sp
10mm
Z2
Z1
hypochordal lobe

2

PLATE 13

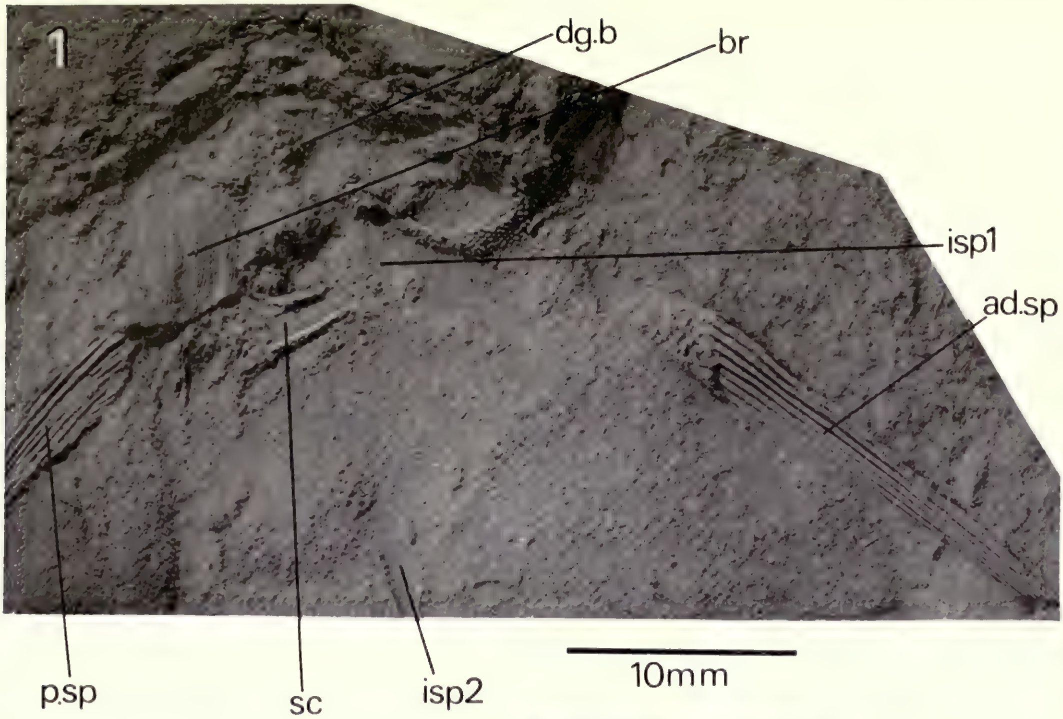
Uraniacanthus spinosus gen. et sp. nov.

Ditton Series, Lower Old Red Sandstone, Wayne Herbert quarry, Herefordshire, England.

FIG. 1. Cast of BM P.16612. Head and shoulder-girdle in dorsal view.

FIG. 2. Cast of BM P.16613. Counterpart of P.16612. Head and shoulder-girdle in ventral view.

Photos: T. W. Parmenter.


1
dg.b
br
isp1
ad.sp
p.sp
sc
isp2
10mm

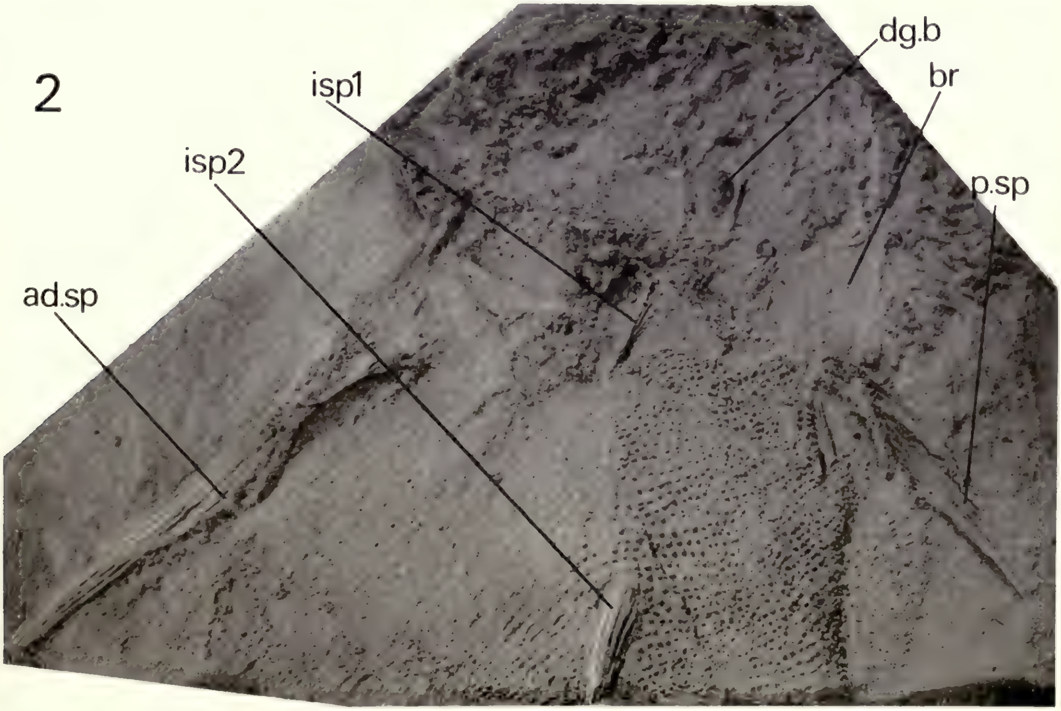

2
dg.b
br
isp1
isp2
p.sp
ad.sp

PLATE 14

Acanthodes bronni Agassiz

Lower Permian, Lebach, Germany. Shoulder-girdle and fin skeleton.

Fig. 1. Cast HU MB24. Photo: U. Samuelson.

Fig. 2. Cast BM P.49980, original HU MB14B. Photo: T. W. Parmenter.

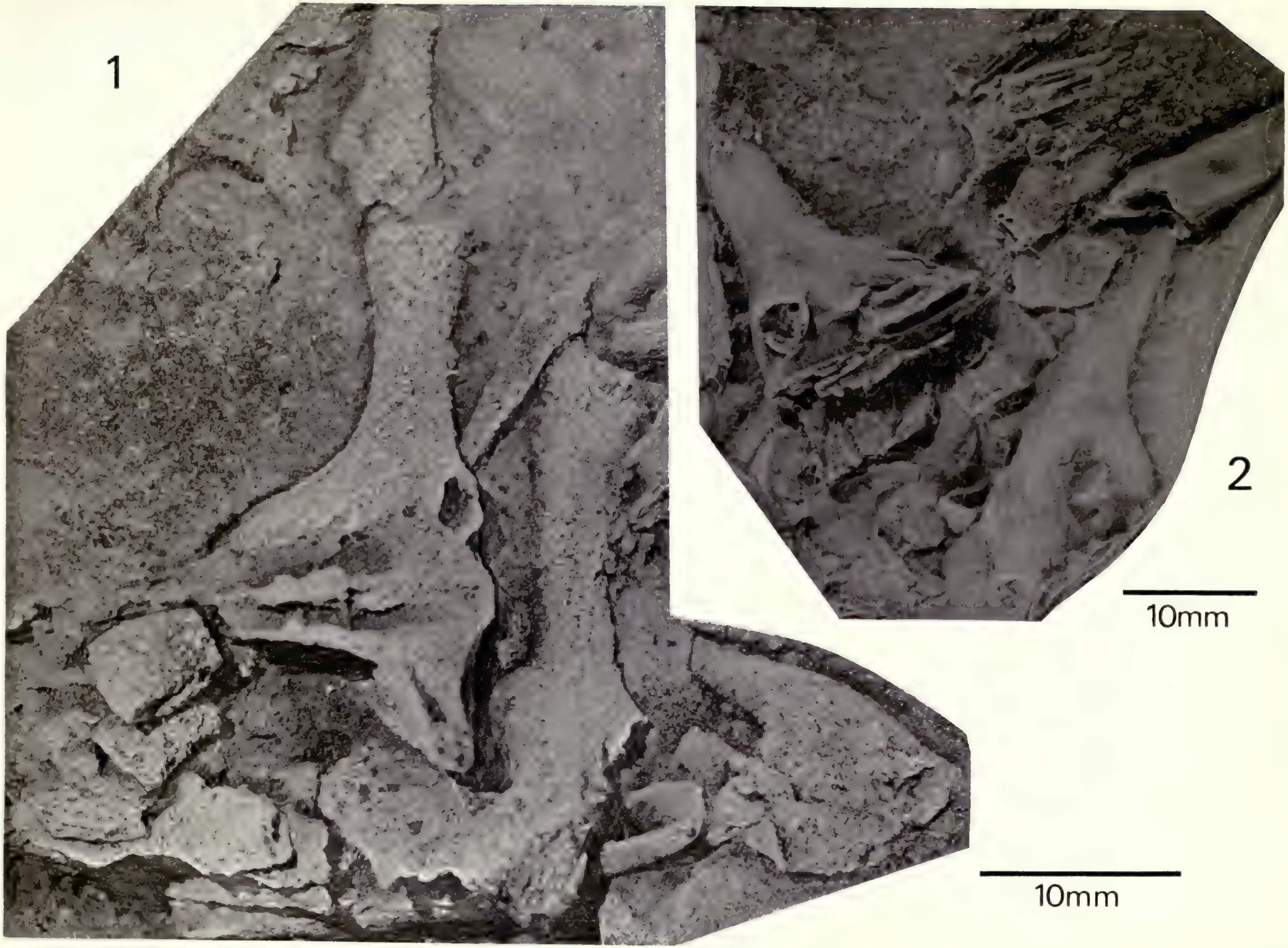

1
2
10mm
10mm

PLATE 15

Euthacanthus sp.

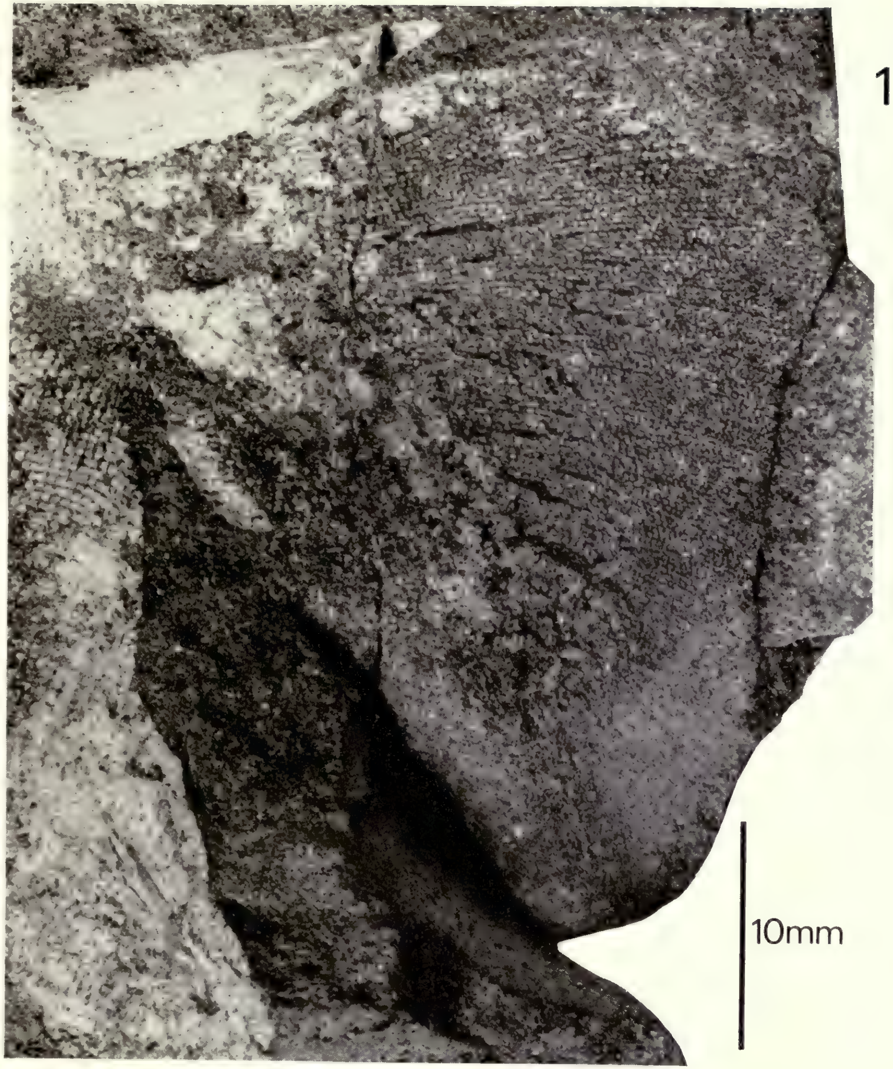
FIG. 1. Pectoral fin with lepidotrichia-like rows of scales. RSM 1971.38. Lower Old Red Sandstone, Angus (?), Scotland.

Cheiracanthus sp.

FIG. 2. Scapula and procoracoid. RSM 1868.19.18. Middle Old Red Sandstone, Tynet Burn, Banffshire, Scotland.

Photos: R. C. M. Thomson.

1



2

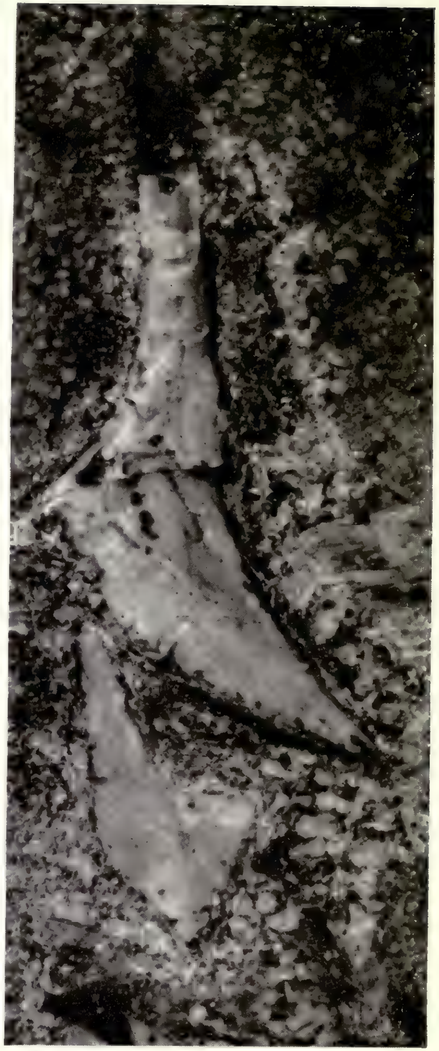


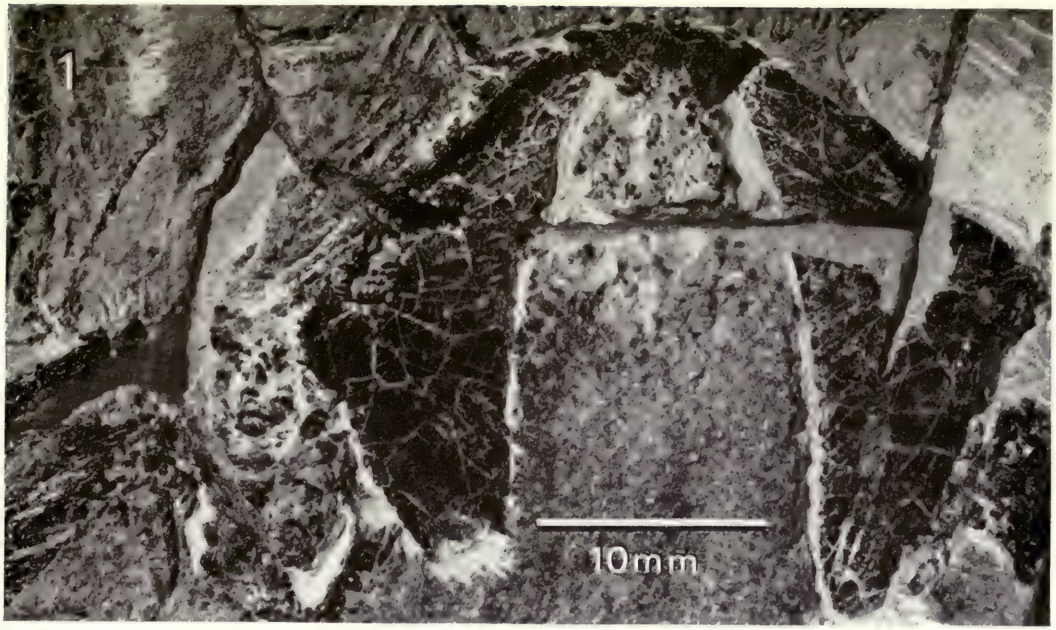
PLATE 16

Parexus falcatus Powrie

FIG. 1. Dermal shoulder-girdle in ventral view. RSM 1891.92.207. Arbuthnott Group, Dundee Formation, Lower Old Red Sandstone, Turin Hill, Angus, Scotland. Photo: R. C. M. Thomson.

Climatius reticulatus Agassiz

FIG. 2. Dermal shoulder-girdle, right side, in ventral view. BM P.6964b. Horizon and locality as for fig. 1. Photo: T. W. Parmenter.


1
10mm

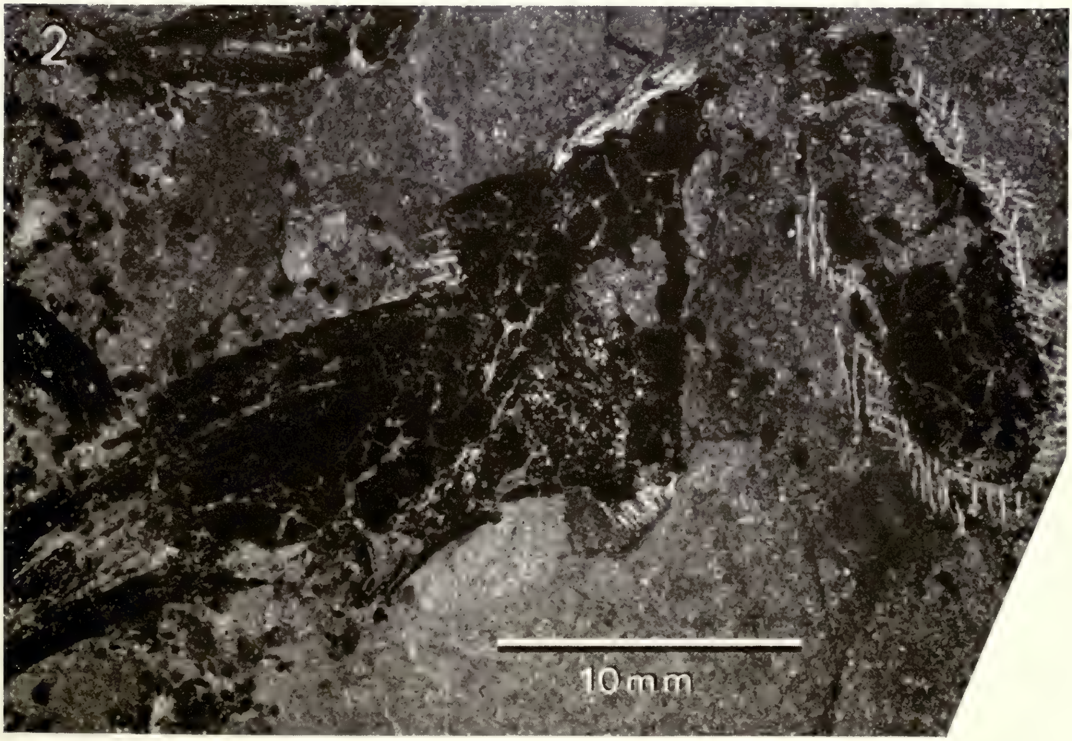

2
10mm

PLATE 17

Sabrinacanthus gen. nov. **arcuatus** (Agassiz)

Ditton Series, Lower Old Red Sandstone, Nass House, Lydney, Gloucester, England.

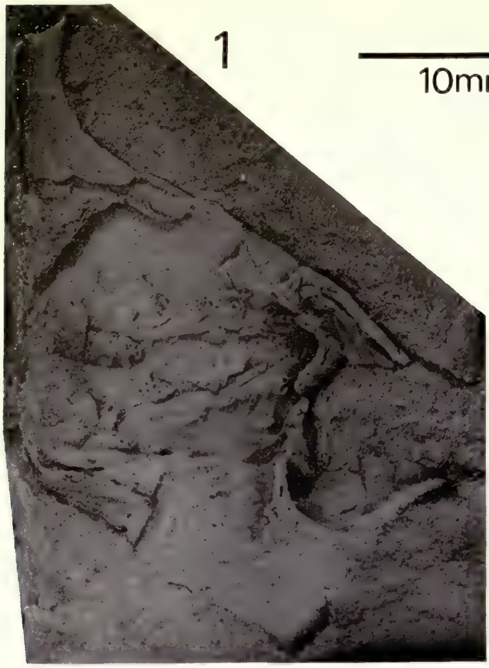
FIG. 1. Cast of BM P.53122a. Scapulocoracoid in mesial view. Use Text-fig. 29D as key-diagram.

FIG. 2. Cast of BM P.53121b. Shoulder-girdle and left pectoral spine in ventral view.

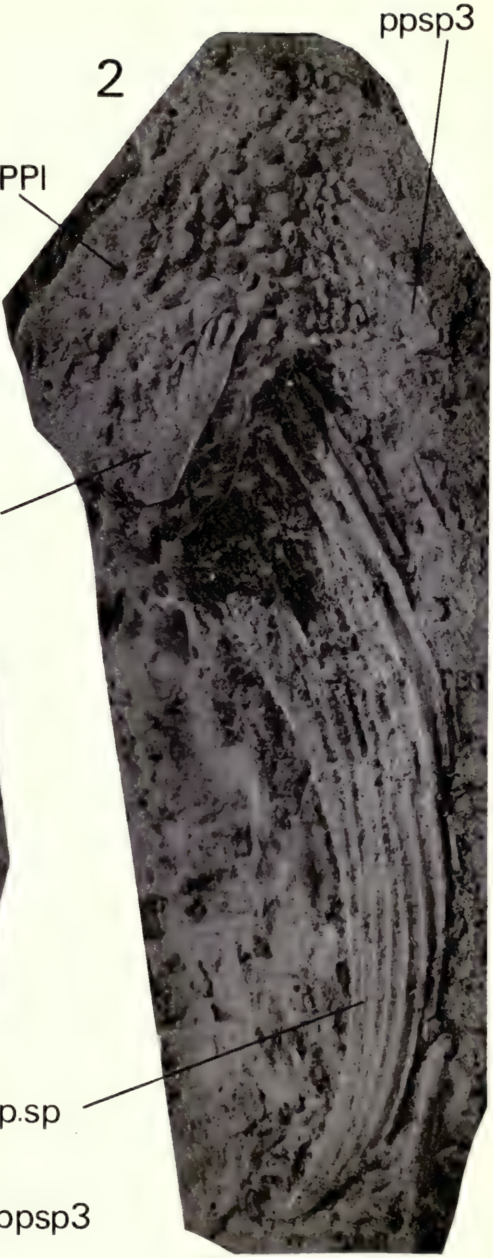
FIG. 3. Cast of BM P.53121a. Counterpart of specimen shown in fig. 2.

Photos: T. W. Parmenter.

1



2


ppsp3
M1,2PPl
isp1
p.sp

3

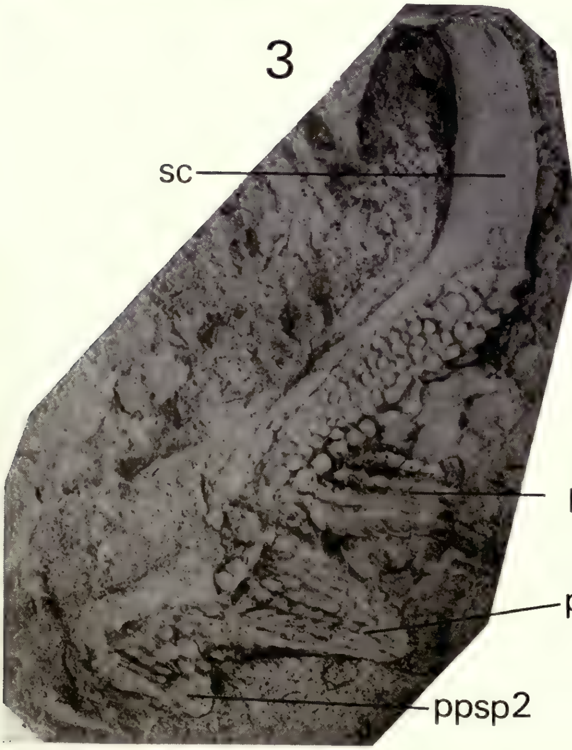

sc
p.sp
ppsp3
ppsp2

PLATE 18

Erriwacanthus manbrookensis sp. nov.

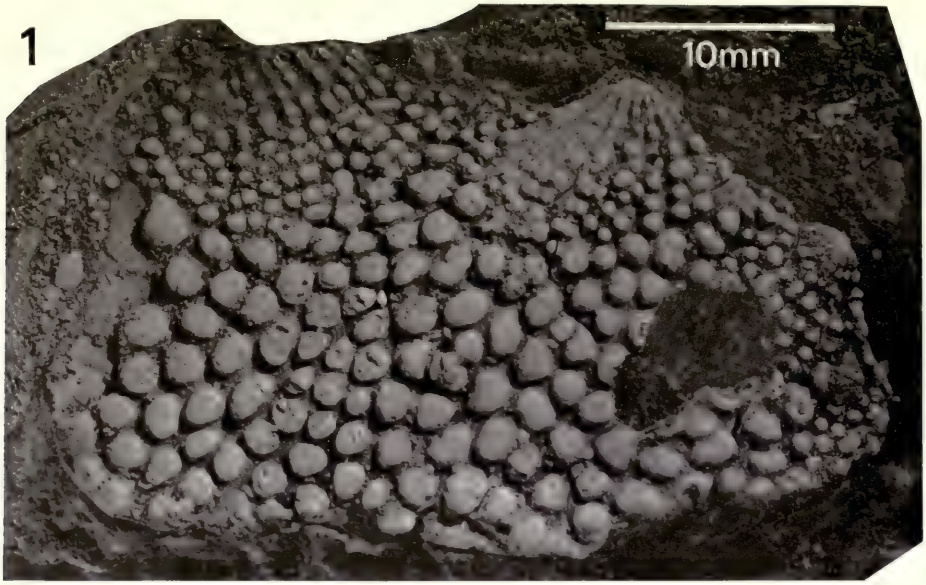
Fig. 1. Ascending left pinnal lamina with prepectoral spines. The keyhole-shaped foramen is due to post-mortem damage. BM P.48984. Downton Series, Red Marl Group, Man Brook 7, Shatterford, Trimpley, Worcestershire.

Euthacanthus macnicoli Powrie

Fig. 2. Right shoulder-girdle. Cast of GSM 88923. Arbuthnott Group, Dundee Formation, Lower Old Red Sandstone, Turin Hill, Angus, Scotland.

Photos: T. W. Parmenter.

1



2

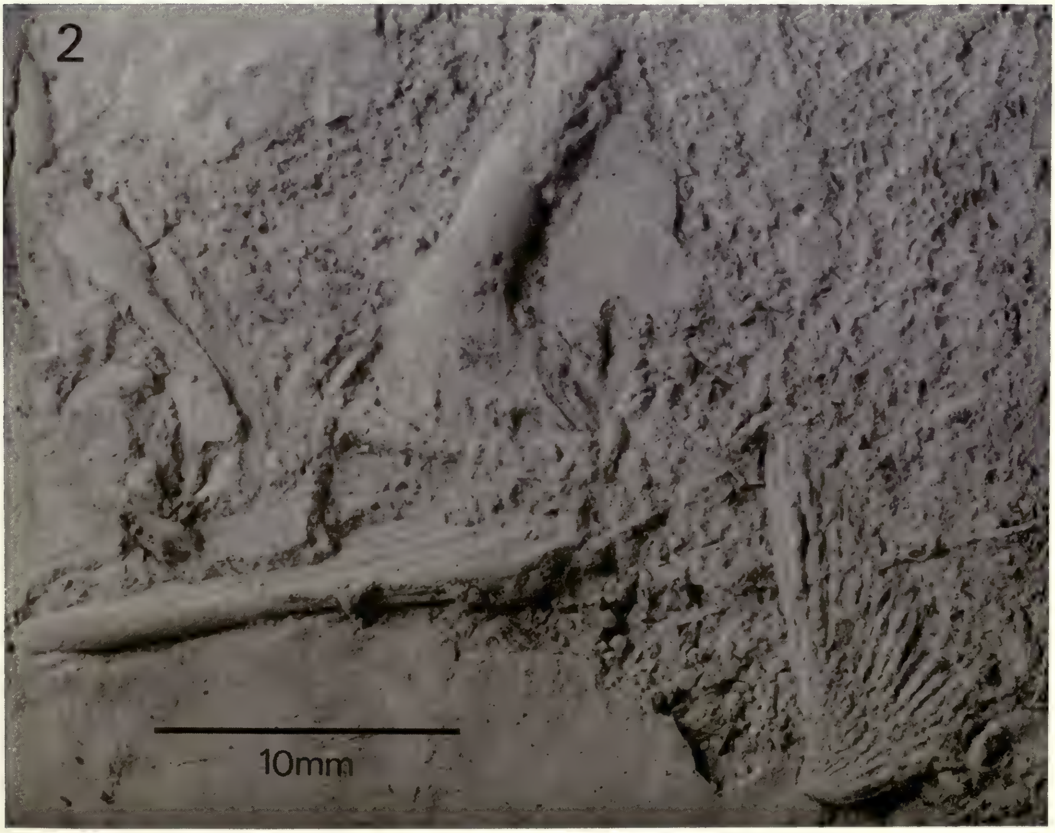


PLATE 19

Ptomacanthus sp. indet 1

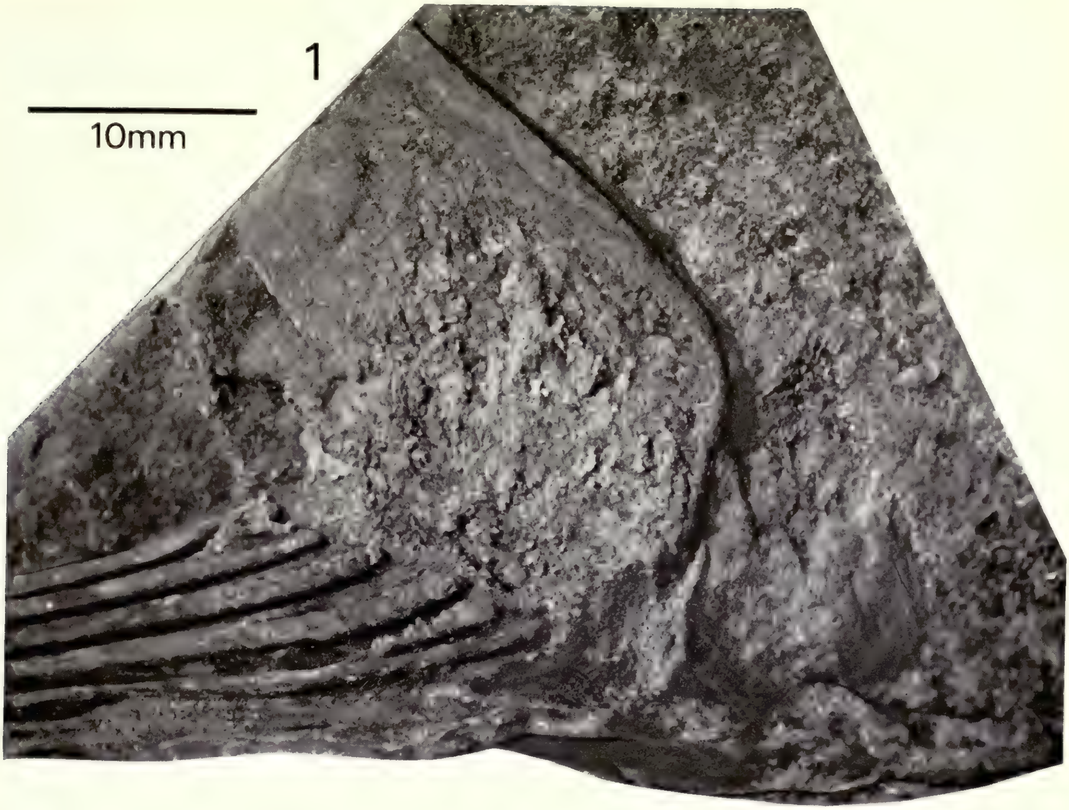
Fig. 1. Cast of BM P.17290 in lateral view. Ditton Series, Castle Mattock quarry, Cladock, Herefordshire, England.

Parexus recurvus Agassiz

Fig. 2. Dermal shoulder-girdle, right side, in lateral view. RSM 1956.14.14. Arbuthnott Group, Dundee Formation, Lower Old Red Sandstone, Turin Hill, Angus, Scotland.

Photos: R. C. M. Thomson.

1



2

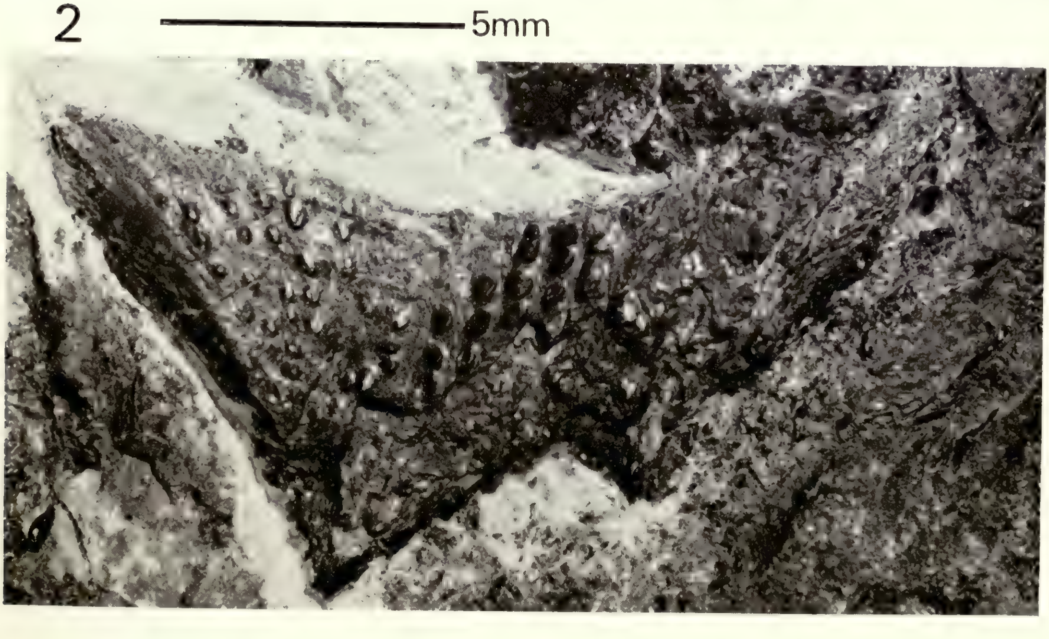


PLATE 20

Ptomacanthus sp. indet 2

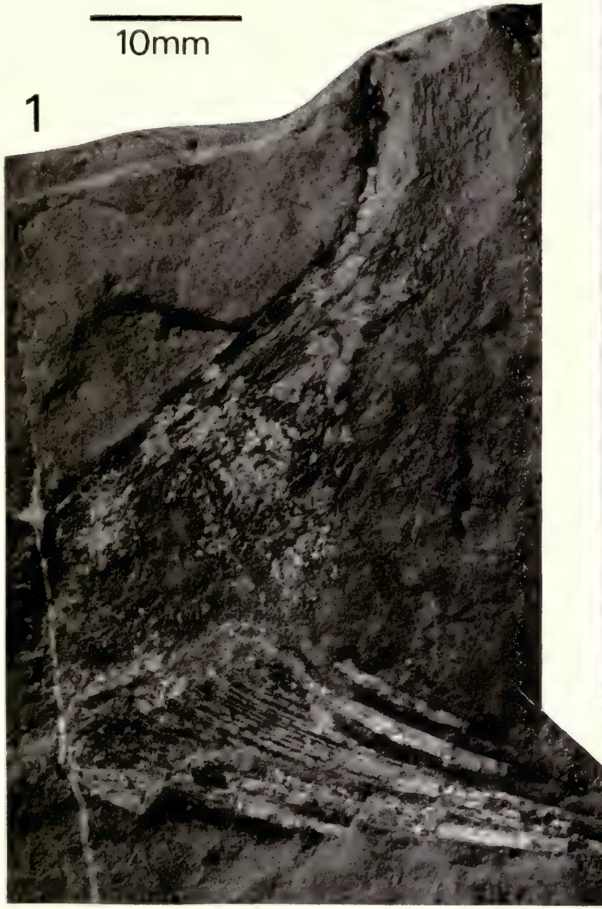
FIG. 1. Shoulder-girdle in lateral view. SMNH P.6841. Dittonian, Zalerzychi, Ukranian SSR.

Cheiracanthus murchisoni Agassiz

FIG. 2. Pectoral fin with 'ceratotrichia'. BM P.9772. Middle Old Red Sandstone, Tynet Burn, Banffshire, Scotland.

Photos: Tordis Junker.

1



2

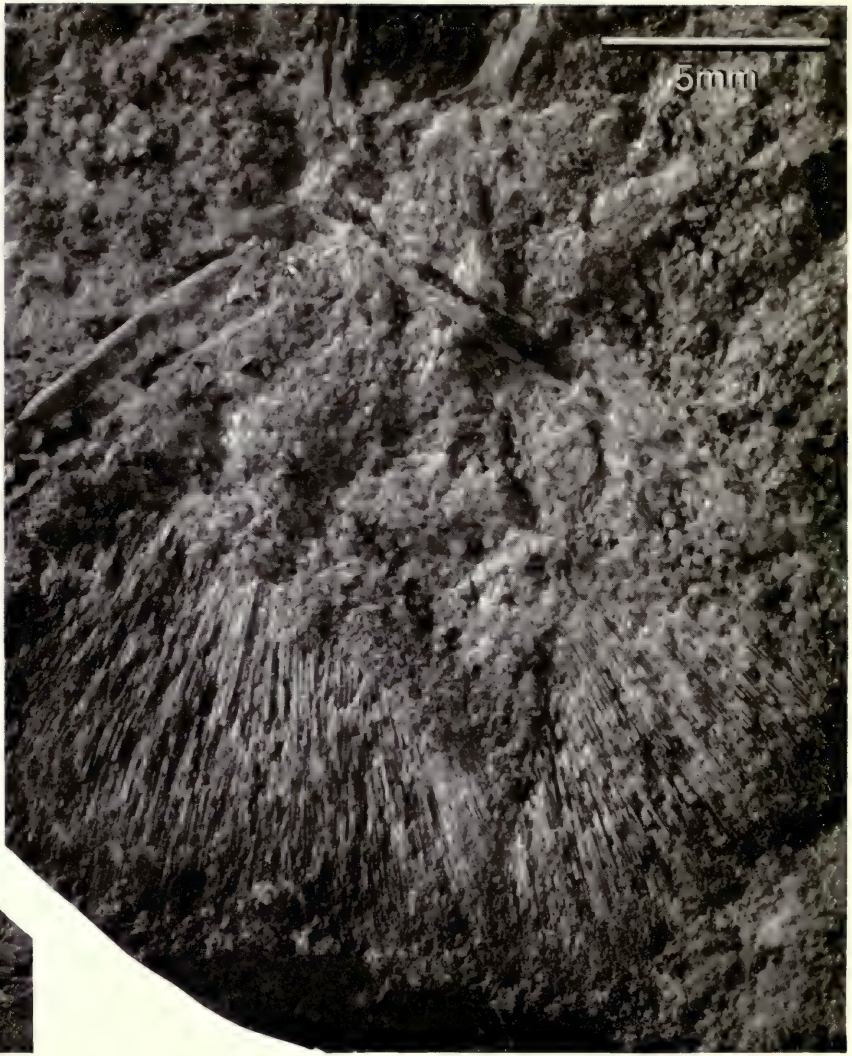


PLATE 21

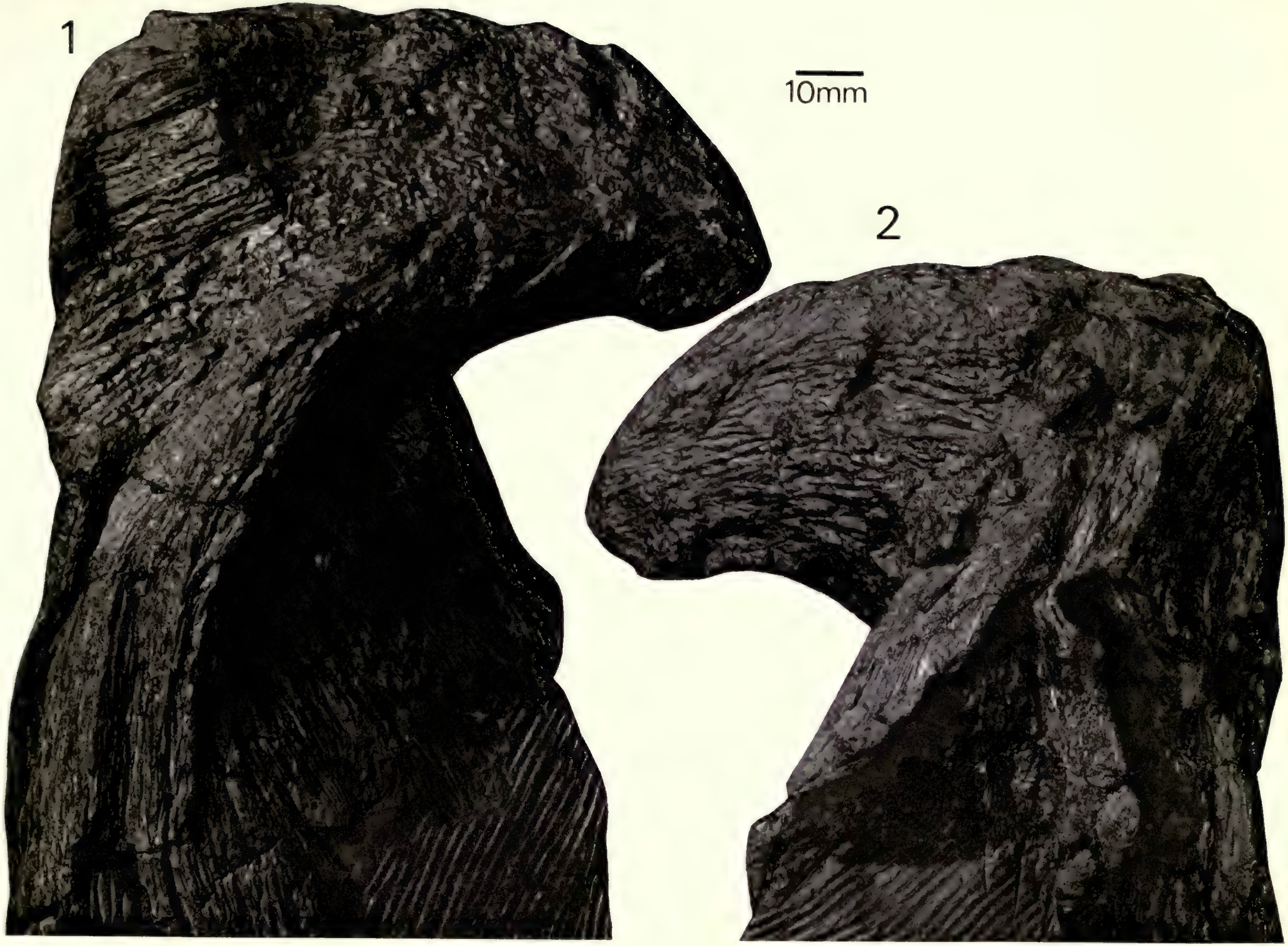
Gyracanthus formosus Agassiz

Paired prepectoral spine and associated plate. BM P.45864. Low Main Seam, Upper Carboniferous, Newsham, Northumberland, England.

Fig. 1. Ventral view.

Fig. 2. Dorsal view.

Photos: Tordis Junker.


1
10mm
2

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THE BRYOZOAN GENUS *SKYLONIA* THOMAS (CHEILOSTOMATA)

A. J. KEIJ

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 24 No. 3
LONDON : 1973

BRIT. NATURAL HIST. -5 SEP 1974

THE BRYOZOAN GENUS *SKYLONIA* THOMAS (CHEILOSTOMATA)

BY

A. J. KEIJ

c/o Shell Internationale Petroleum Maatschappij B.V., The Hague, Netherlands

Pp. 215–233; 4 *Plates,* 3 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 24 No. 3
LONDON: 1973

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THE BRYOZOAN GENUS *SKYLONIA* THOMAS (CHEILOSTOMATA)

By A. J. KEIJ*

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SYNOPSIS

The anascan genus *Skylonia* Thomas is monographed, comprising six species of which four new species and two subspecies are erected here, ranging from the Middle Eocene to Late Miocene, possibly Pliocene. First known from the Eocene of Cuba and Mexico, *Skylonia* achieved a circumtropical distribution by Miocene times.

I. INTRODUCTION AND ACKNOWLEDGEMENTS

THE genus *Skylonia* was introduced by Thomas in December 1961 for a problematical fossil, *Skylonia mirabilis*, found in the Lower Miocene of Kenya. Thomas compared *Skylonia* with the Bryozoa but rejected its affinities with this group. Almost simultaneously Sandberg (1962) introduced the genus *Fusicanna* for a Miocene species, *Fusicanna dohmi*, of the Dominican Republic and placed this genus in the bryozoan family Fusicellariidae (Cheilostomata, Ascophora).

The author's interest in the genus *Skylonia* was aroused, for while employed as a palaeontologist for Brunei Shell Petroleum Co., in northwestern Borneo, he had found these peculiar spindles in the Tertiary sediments of Sarawak and Sabah (Malaysian Borneo) and Cebu (Philippines), prior to the publication of the papers by Thomas and Sandberg. In 1962 and 1963 all the East Asian material was presented to the British Museum (Natural History) in London to enable Dr H. D. Thomas to prepare a monograph on the genus. Meanwhile additional material of a related, but apparently undescribed, genus had been found by Dr Y. Nagappa in the Eocene of Assam and by Dr R. Lagaaij in the Eocene of Belgium and of Libya together with *Skylonia* species from the Eocene of Cuba and the Neogene of Nicaragua and Indonesia. Dr D. A. J. Batjes supplied some Miocene specimens from Trinidad, Dr R. J. Scolaro from the Lower Miocene of Florida. The present author found some specimens in the Middle Eocene of Mexico and in the Upper Neogene of Fiji. Unfortunately, owing to the untimely death of Dr Thomas, the planned monograph did not materialize. This was the situation when the Trustees of the British Museum kindly allowed the author to study their *Skylonia* collection.

* C/o Shell Internationale Petroleum Maatschappij B.V, The Hague, Netherlands.

During this study valuable additional topotype material of *Skylonia mirabilis* Thomas was received from the British Petroleum Company Ltd and of *Skylonia dohmi* (Sandberg) from Dr P. A. Sandberg.

The larger part of the *Skylonia* material here described has been deposited in the British Museum (Natural History), London (numbers Z 934–956, 978–984 and D 51492–51853, 51855–51869) and the remainder in the Rijksmuseum van Geologie en Mineralogie at Leiden, Netherlands (numbers RGM 172524–172547).

I wish to thank all who contributed material for my study, especially the British Museum (Natural History) in London, the Union Oil Company of California, Dr P. A. Sandberg (Urbana, Illinois, U.S.A.) and Dr W. J. Clarke of the British Petroleum Company Ltd. I am particularly grateful to Dr R. Lagaaij and Miss P. L. Cook, who both critically read and discussed the manuscript. Permission from Shell Internationale Petroleum Maatschappij B.V. to publish this paper is gratefully acknowledged.

II. SYSTEMATIC AFFINITIES OF *SKYLONIA*

The systematic position of *Skylonia* within the Cheilostomata invites some comments. In the controversy between Thomas (1961) and Sandberg (1963) as to whether *Skylonia* is a bryozoan or not, I am inclined to side with the latter. The following characters, in my opinion, support the bryozoan nature of *Skylonia* (see also Sandberg 1963, p. 17). (1) Colonies consist of elongate, erect spindles apparently originally connected to an incrusting, e.g. stolonate, base by a cuticular joint. (2) The camerate structure is bryozoan-like. The chambers are quadrate to hexagonal in outline on the outer surface and they are similar in size to those found in Bryozoa. (3) The chambers are arranged in a number of longitudinal rows around the axis of the spindle. (4) Chambers alternate in adjacent rows. (5) Chambers inter-connect by simple communication-pores. (6) Each chamber has a single aperture on the outer surface of the spindle. (7) Openings interpreted as rootlet pores occur at the proximal and distal extremities of the spindles.

I agree with Sandberg that *Skylonia* belongs to the Cheilostomata. Sandberg, however, placed *Skylonia* in the Ascophora, whereas I am inclined to assign it to the Anasca on account of two additional characters. The first is that spindles of *Skylonia* show at their proximal end, which is often somewhat curved, a single large initial zooecium, the " anascaform zooecium " of Sandberg (1962, p. 65). A similar wide open and slightly tilted initial zooecium occurs in several Upper Cretaceous or Lower Tertiary Anascan species, such as *Encicellaria hofkeri* Keij, *Stamenocella oculata* (Ulrich and Bassler), " *Cellaria* " *mucronata* Meunier & Pergens, and in more complete specimens of the species referred to " *Smittipora* ? " by Labracherie (1968, p. 315). The first species occurs in the Maastrichtian of Maastricht, the second in the Paleocene Vincentown Limesand of New Jersey, the third in the Montian " Calcaire de Mons " in a boring near Mons, Belgium, and the fourth in the Bartonian blue marls of the Falaise de Handia near Biarritz in France. In the first two species there is no evidence of ramification, in the third species at least lateral ramification occurs, and in the fourth species distal ramification only, via chitinous joints, can be inferred from the paired basal rami at the distal extremity of the internodes. In *Skylonia* there is no evidence of distal jointing.

The second characteristic feature is the frontal closure of the zooecia. A more or less dome-shaped calcareous lamella is developed with a small to fairly large, circular to transversely elongate opening in its centre (*vide* the " blind zooecia " of Canu & Bassler 1920, text-fig. 23). This feature, too, is known only from a number of anascan genera. In some of these genera an arcuate impression is sometimes observed distal to the central opening, corresponding in shape and position to the distal outline of the operculum, and indicating that closure developed just beneath the frontal membrane. Genera with calcareous closures in which such " opercular scars " occur are marked with an (*) in table 1; others, including *Skylonia*, in which they are definitely absent, are marked with a (−). It would seem, therefore, that in these various genera calcareous closures do not always develop in identical fashion.

In *Skylonia* all zooecia in the spindle, with the exception of the initial one, are as a rule closed, although spindles without calcareous closures, presumably representing unaltered opesiae, do occur (Pl. 1, fig. 13; Pl. 2, fig. 2; Pl. 3, fig. 9; Pl. 4, figs. 3, 6 and 7). It appears that the spindles are either entirely with, or devoid of, such calcareous closures, in contrast to the situation found in the Maastrichtian *Encicellaria hofkeri* Keij, where some spindles had their proximal zooecia closed and their distal zooecia still open and probably functioning at the time of death. Closed zooecia are found quite commonly in species of genera belonging to the suborder Anasca, and especially in the division Malacostega. They occur both in incrusting and in articulating, erect, species. A survey made by Dr Lagaaij of illustrations in literature and of his extensive collection produced examples in species belonging to the following genera (table 1).

Table 1

Anascan genera in which calcareous closures may occur

Division Malacostega	
Family Membraniporidae	*Biflustra*(−), *Conopeum*(*), *Vincularia*(*)
Cupulariidae	*Cupuladria*(*)
Electridae	*Pyripora*(*)
Hincksinidae	*Ellisina*(?), *Setosellina*(−)
Calloporidae	*Callopora*(?), *Membraniporidra*(?), *Mollia*(−), *Parellissina*(?), *Planicellaria*(*), *Retevirgula*(?), *Stamenocella*(*)
Fusicellariidae	*Fusicellaria*(−), *Encicellaria*(−)
Skyloniidae	*Skylonia*(−)
Division Coilostega	
Family Onychocellidae	*Thyracella*(*)
Microporidae	*Vibracella* (*Discovibracella*)(*)
Division Cellularina	
Family Farciminariidae	*Nellia*(*)
Scrupocellariidae	*Scrupocellaria*(*)

(*): opercular scar observed; (−): opercular scar not observed; (?): unknown.

A few examples of closed zooecia with or without opercular scar are figured here, i.e. *Nellia tenuis* Harmer (Recent, South China Sea—Pl. 1, fig. 7), *Scrupocellaria milneri* Canu & Bassler (Oligocene, Byram type locality, U.S.A.—Pl. 1, fig. 8), *Stamenocella oculata* (Ulrich & Bassler) ? (=*Planicellaria oculata* Ulrich & Bassler 1907, non d'Orbigny 1851) (Paleocene, Vincentown limesand, U.S.A.—Pl. 1, fig. 3), *Planicellaria fenestrata* d'Orbigny (Thanetian, Musitu, Prov. Vitoria, Spain—Pl. 1, fig. 1), *Vincularia fragilis* (Defrance) (Lower Lutetian of Nalinnes, Belgium—Pl. 1, fig. 2). This phenomenon may even have led to the introduction of new species. Two examples are known from the older literature. *Planicellaria fenestrata* d'Orbigny (1851, pp. 37–38) and *P. oculata* d'Orbigny (1851, p. 37) were described by d'Orbigny from the same locality, the Maastrichtian of Néhou (Manche) in NW France. I strongly suspect that *P. oculata* represents specimens of *P. fenestrata* of which the zooecia were closed-off by a calcified lamella leaving only a relatively small opening in the centre. *P. oculata* was designated the type species of the genus. A similar situation is suspected for two Middle Miocene species of *Scrupocellaria* described by Reuss (1848) from the Leitha Kalk of Eisenstadt. *Scrupocellaria schizostomata* (Reuss) (1848, pl. 9, fig. 9) might well represent *S. granulifera* (Reuss) (1848, pl. 9, fig. 6) with the zooecia occluded by calcareous lamellae.

III. ENVIRONMENT

Skylonia is often found in association with larger benthonic Foraminifera such as the Middle Eocene *Polylepidina chiapasensis* Vaughan in Mexico, or *Operculina–Lepidocyclina–Amphistegina* species in the Miocene of Borneo, or *Miogypsina–Lepidocyclina–Taberina* in the Middle Miocene of Kenya. The living larger benthonic Foraminifera, such as the infaunal *Operculina* and the epifaunal *Amphistegina*, *Heterostegina* and *Peneroplis* all carry symbiontic zooxanthellae in their protoplasm and are therefore restricted to the photic zone of shallow, tropical seas.

A characteristic assemblage of other Bryozoa is found together with *Skylonia*, consisting of species of *Nellia*, *Vincularia*, *Margaretta*, *Crisia* and *Poricellaria* (see table 2). These are all cellariiform genera, i.e. having erect, branching, flexible (jointed) colonies, which are attached to their substratum of rock, indurated sediment, plants etc. by rootlets. According to Stach (1936, p. 63) the cellariiform growth form " is adapted for life in the littoral zone ". The kinetic energy of the water must have been moderate, sufficiently high to prevent mud from settling and choking the bottom fauna, but not so high that it detached the bryozoan colonies.

The above evidence suggests that *Skylonia* lived in shallow, tropical to subtropical holomarine seas at depths estimated not to have much exceeded 50 m.

IV. DISTRIBUTION

The oldest known *Skylonia* species occurs in the Middle Eocene of Mexico and Cuba and the Upper Eocene of Cuba (*Skylonia bermudezi* n. sp.) (see text fig. 1). No Oligocene *Skylonia* species are known yet. In the Early Miocene, however, *Skylonia* was established in Borneo with *Skylonia sarawakensis* n. sp. (see text figs. 1 and 2) and *S. sandbergi* n. sp., and in Trinidad, Nicaragua and the Dominican

TABLE 2

Bryozoan assemblages found associated with *Skylonia*

● : dominant
○ : common
+ : rare

	Middle Eocene—Mexico	Lower Miocene—Nicaragua			Sarawak							Middle Miocene—Madura	Middle Miocene—Kenya	Middle Miocene—Trinidad	Sabah		Upper Miocene—Cebu	Upper Miocene/Lower Pliocene—Fiji
					Lower Miocene	Lower Miocene	Lower Miocene	Lower Miocene	Lower Miocene	Middle Miocene	Middle Miocene				Upper Miocene	Upper Miocene		
		500 m	560 m	640 m	Bu 509	Ca 53	Ca 54	R 860	R 861	J 1065	Mu 823	Be 1421	REC 2082	DB 268	Jo 121	Mt 2196	My 1994	DEV 18
Canda												+						+
Cellaria												+						
Celleporidae			+	+								○		+				
Crisia	○				○	+	○		●			●	+					●
Cyclostomes indet.								+									+	
Gemellipora														+				
Idmonea	○						○											+
Lichenopora												+						
Margaretta		○	○	+	+					○	○	●	+				+	+
Metrarabdotos		●	●	●										+				
Nellia	●	●	●	●	○	●	●	+	+	+		●	●	●				+
Pasythea	●		+									●	○				+	
Poricellaria	+							+				●	+					+
Savignyella												+						
Scrupocellaria			+									+	+	+	+			+
Semihaswellia	○																	
Sertella												●						+
Skylonia	○	+	+	+	+	+	+	+	+	+	+	+	○	+	+	+	+	+
" Smittipora "	○																	
Steganoporella												+						
Thalamoporella	○?		+	+								○		+				+
Tremogasterina				+														
Vibraculina			+															
Vincularia	●				+	+	+				+	●	●		●	+	●	+
Vittaticella	+											●	+	+				+

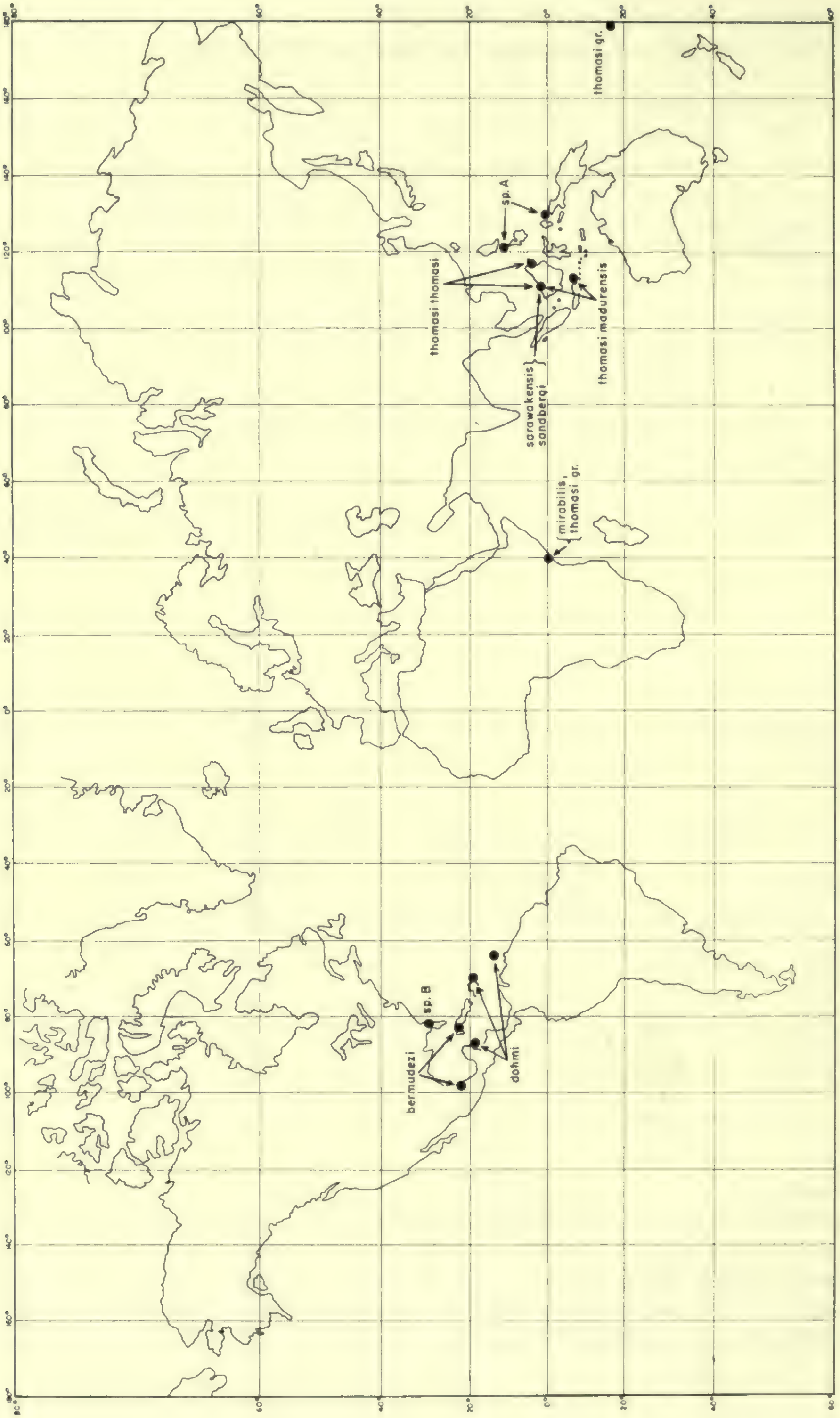
thomasi gr.
sp. A
thomasi thomasi
sarawakensis
sandbergi
thomasi madurensis
mirabilis,
thomasi gr.
sp. B
bermudezi
dohmi
80°
60°
40°
20°
0°
20°
40°
60°
180°
160°
140°
120°
100°
80°
60°
40°
20°
0°
20°
40°
60°
80°
100°
120°
140°
160°
180°

FIG. 1. Distribution of *Skylonia* species.

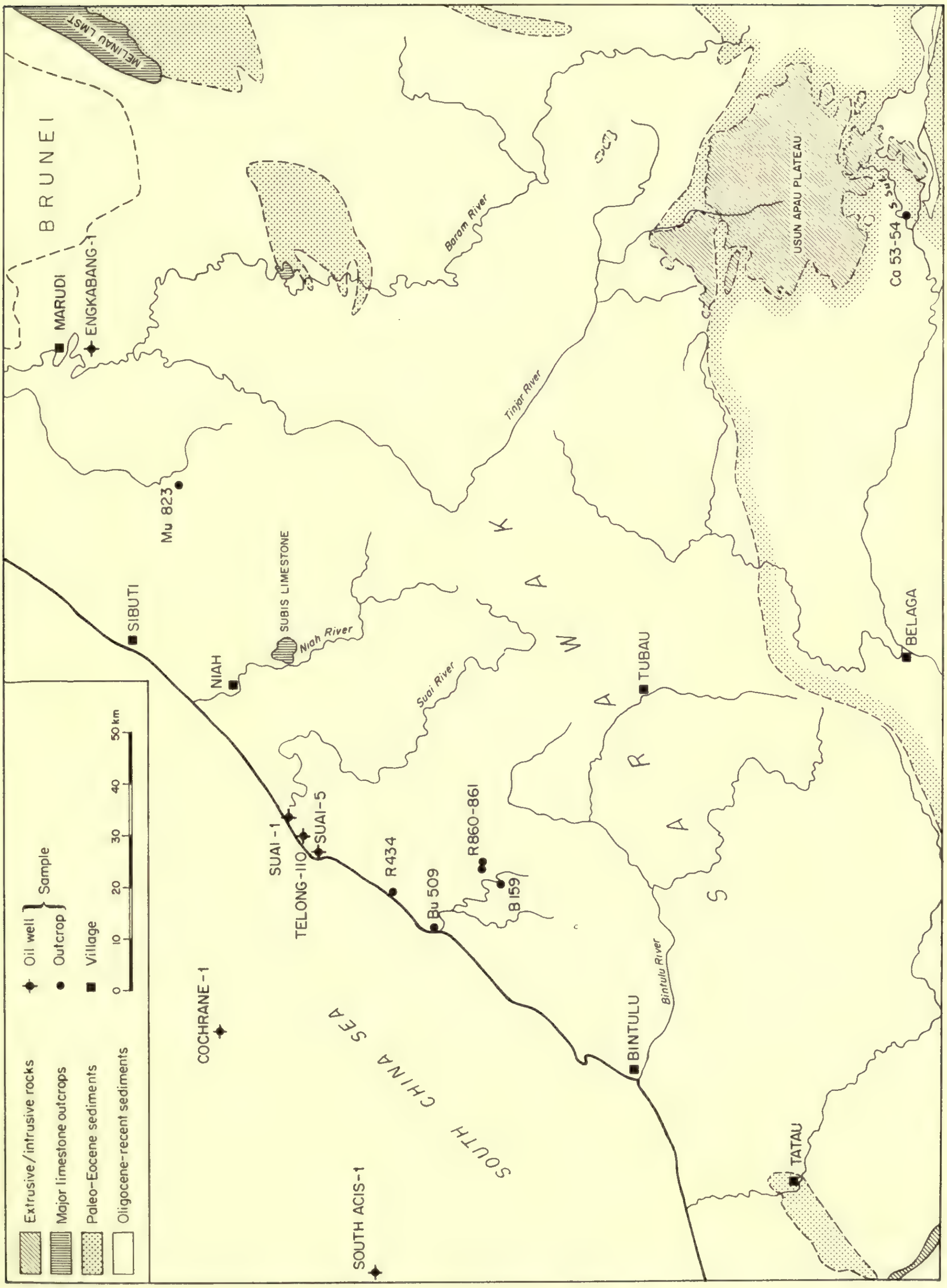
BRUNEI
MELINAU LMST
MARUDI
ENGKABANG-1
Baram River
Tinjar River
USUN APAU PLATEAU
Ca 53-54
Mu 823
SUBIS LIMESTONE
Niah River
SIBUTI
NIAH
Suai River
SARAWAK
TUBAU
BELAGA
SUAI-1
SUAI-5
TELONG-110
R434
R860-861
Bu 509
B159
Bintulu River
BINTULU
TATAU
COCHRANE-1
SOUTH ACIS-1
SOUTH CHINA SEA
Extrusive/intrusive rocks
Major limestone outcrops
Paleo-Eocene sediments
Oligocene-recent sediments
Oil well
Outcrop
Sample
Village
0
10
20
30
40
50 km

FIG. 2. *Skylonia* localities in Sarawak, Malaysian Borneo.

Republic with *S. dohmi* (Sandberg). *S. sandbergi* ranged up into the Middle Miocene, when it was replaced by *S. thomasi* n. sp., a species known with two subspecies and a few related forms from Borneo, the Philippines, Indonesia, Fiji and Kenya. The youngest representatives of this species probably reached up into the Pliocene (Kenya, Indonesia). During the Middle Miocene the type-species of the genus, *S. mirabilis* Thomas, lived in Kenya. Fragments of specifically unidentified forms were found in the Miocene of Florida (U.S.A.), i.e. *Skylonia* sp. B, and the Upper Miocene of Eastern Indonesia and the Philippines, i.e. *Skylonia* sp. A, and they may well belong to still undescribed species.

TABLE 3

Ranges of *Skylonia* species

	Eocene		Oligocene			Miocene			Pliocene
	M.	Upper	L.	M.	U.	Lower	M.	Upper	
Skylonia bermudezi n. sp.	—	—							
sarawakensis n. sp.					—	—			
sandbergi n. sp.						—	—		
dohmi (Sandberg)						—			
mirabilis Thomas							—		
thomasi n. sp.							—	—	– ?

V. SYSTEMATIC DESCRIPTIONS

Order CHEILOSTOMATA Busk, 1852

Suborder ANASCA Levinsen, 1909

Family **SKYLONIIDAE** Sandberg, 1963

Genus ***SKYLONIA*** Thomas, 1961

(Synonym, ***FUSICANNA*** Sandberg, 1962)

TYPE SPECIES. *Skylonia mirabilis* Thomas, 1961.

DIAGNOSIS. Skyloniidae with zoarium composed of elongate spindles, tapering symmetrically and with zooecia arranged quadriserially. A single anascaform zooecium at proximal end. Zooecia usually with frontal closure, each with a small, central, usually circular or transversely elongate aperture. No ovicells or avicularia.

REMARKS. *Skylonia*, originally introduced as a problematical fossil, bears only a remote resemblance to other genera of the Cheilostomata Anasca, e.g. *Fusicellaria* d'Orbigny, 1851, or *Encicellaria* Keij, 1969.

RANGE. Middle Eocene to Late Miocene, probably even Pliocene.

DISTRIBUTION. Circumtropical and subtropical.

Skylonia mirabilis Thomas

(Pl. 3, figs. 10–13)

1961 *Skylonia mirabilis* Thomas, 360–363, pl. 13.
1963 *Skylonia mirabilis* Thomas; Sandberg, 4–14, fig. 3—nos. 6 and 7.

Distribution. Middle Miocene of Gaji Hill, west of Malindi and in Ngombeni quarry at Mafia Island, Kenya. According to Dr W. J. Clarke also occurring in sediments of approximately the same age on Zanzibar Island, but no material was available for study.

Diagnosis. *Skylonia* with spindles with twelve to fifteen hexagonal zooecia per longitudinal row, with apertures in the widest part of the spindle only slightly wider than high and situated at the crest of the domal elevation of frontal wall.

Remarks. The spindles, which are 1·4 to 1·7 mm long, 0·29 to 0·36 mm wide (Sandberg, p. 7), are narrow and taper evenly towards both ends, with the proximal end often somewhat curved. The hexagonal shape of the zooecia and the simple domal elevation around the circular to somewhat transversely elongate aperture appear to characterize this species. A tendency was observed towards the development of low knobs flanking the apertures in the widest part of the spindles. In the few spindles in which the proximal end is not broken off it appears that this species has proximal pores in the initial zooecia of the lateral rows (Pl. 3, figs. 11b and 13). One specimen was observed to have a pore above the initial zooecium (Pl. 3, fig. 13). Communication-pores were found by Thomas between adjacent zooecia in the same vertical row, but not between zooecia of adjacent rows. This must be due to the mediocre preservation of the Kenya specimens because they do occur in other species, e.g. *Skylonia dohmi* and *S. thomasi*.

The material is deposited in the British Museum (N.H.) under numbers Z 934–956, 859–894 and in Leiden under RGM 172533–172535.

Skylonia bermudezi n. sp.

(Pl. 2, figs. 1–4)

Name. In honour of Prof. Dr P. J. Bermudez, Caracas, Venezuela.

Type locality. Jabaco at 4½ km west of Guanajay, Province of Pinar del Rio, Cuba (loc. B 337A of Bermudez, 1950, p. 240).

Type stratum. Jabaco Formation of Late Eocene age.

Holotype. Spindle in slide D 51855 (British Museum).

Paratypes. Fourteen spindles from type locality (D 51856–51869) and (RGM 172524), one fragment of a spindle from the same Formation collected at ½ km south of Ingenio Saratoga, Matanzas Province, Cuba (Bermudez loc. B 322) (RGM 172525), and one spindle of Middle Eocene age derived from the Loma Candela Formation at Loma Candela, Province of Pinar del Rio, Cuba (Bermudez loc. B 261, 1950, p. 244).

Diagnosis. *Skylonia* with spindles with seven to ten zooecia per vertical row, apertures with well-developed raised rim and with one to three frontal pores in the terminal zooecia at both ends of spindle.

Description. Spindles are widest near the middle, varying in width between 0·46 and 0·68 mm, and sometimes slightly curved, with seven to ten zooecia per vertical row. The frontal closure is mostly rectangular in outline but in some spindles the proximal and distal boundaries are arched. The largest zooecia are found near the middle of the spindles, widths varying from 0·32 to 0·41 mm, and lengths varying from 0·15 to 0·19 mm.

The apertures are nearly circular to somewhat transversely elliptical, 0·05 to 0·07 mm in diameter, surrounded by a conspicuous raised rim (Pl. 2, fig. 3) or by a less well-developed rim supplemented by two low knobs flanking the aperture (Pl. 2, fig. 1). These knobs are best developed in the middle part of the spindle.

Frontal pores are present in the first and last two zooecia of each row, there are usually three per zooecium, but occasionally only one or two were observed.

REMARKS. In the Middle Eocene Lower Guayabal Formation of the Rio Tecolutla area of Mexico, some badly preserved spindles were found (Pl. 2, fig. 4—RGM 172526–27) which are somewhat differently shaped but very probably belong to *Skylonia bermudezi* n. sp. The number of zooecia per vertical row is slightly lower, i.e. six to nine. No raised rim round the apertures or paired flanking knobs were found, nor raised edges of the frontal plates, because the spindles were worn smooth. More than one frontal pore is present at least at one end of each spindle. This Mexican sample was collected by Mr R. Wright Barker in the upstream area of the Rio Tecolutla from the south bank of the Chumatlan River, a few miles upstream from its confluence with the Rio Espinal, State of Veracruz.

Skylonia dohmi (Sandberg)

(Pl. 2, figs. 5–7)

1962 *Fusicanna dohmi* Sandberg, 65, figs. 12–16.
1963 *Skylonia dohmi* (Sandberg), Sandberg : 1–19, figs. 1–5.

DISTRIBUTION. Lower Miocene Baitoa Formation of the Dominican Republic and the Middle Miocene Biche limestone Member of the Brasso Formation of Biche quarry, Trinidad (samples DB 268 and WHB 153). Also in unnamed Lower Miocene beds in Union Oil Company of California off-shore boring Martinez-Reef no. 1 at 500, 560 and 640 m depth, off-shore Nicaragua (N 14°34′09″–W 82°32′11″).

DIAGNOSIS. *Skylonia* with spindles with thirteen to fifteen zooecia per longitudinal row, proximal frontal pores in end zooecia of all four rows, the apertures in the middle part of each spindle transversely elliptical and with a conspicuous raised rim.

REMARKS. This species was described in detail by Sandberg (1963).

The preservation of the Dominican specimens is excellent, that of those from Trinidad very poor, but they retained enough of their features to allow a specific allocation.

Of the Indo-malaysian species, *S. thomasi* n. sp. resembles *S. dohmi* most closely, but differs in having fewer zooecia per vertical row (only eleven to thirteen) and in having a less well-developed raised rim round the apertures, although some spindles have two low knobs flanking the aperture (Pl. 2, fig. 6). The American species, moreover, has proximal frontal pores in the end zooecia of all four rows, whereas they are restricted to the lateral rows in all the Indo-malaysian species.

The material is deposited in the British Museum under numbers Z 978–984, D 51492–51495 and in Leiden under RGM 172528–532.

Skylonia sandbergi n. sp.

(Pl. 1, figs. 10–13)

NAME. In honour of Dr P. A. Sandberg, Urbana, Illinois, U.S.A.

TYPE LOCALITY. Cochrane well 1, off-shore Sarawak at N 5°54′38″–E 113°07′08″, South China Sea.

TYPE STRATUM. Unnamed formation at 7519 ft depth and of Early Miocene age.

HOLOTYPE. Spindle (D 51709).

PARATYPES. Several spindles and fragments (D 51710–51853 and RGM 172536–540) from the following localities in Sarawak: Suai well 1 (400–1903 ft depth)—Early Tertiary *f* or Early Middle Miocene; Telong corehole 110 (265–274 ft depth)—Late Tertiary *e* or Early Miocene; Cochrane well 1 (4120–7520 ft depth)—Late Tertiary *e* to Early Tertiary *f* or Early to Middle Miocene; Engkabang well 1 (3567–3890 ft depth)—Late Tertiary *e* or Early Miocene; South Acis well 1 (4600–4650 ft depth)—Early to Middle Miocene; outcrop sample J 1065—Early Tertiary *f* or Early Middle Miocene; outcrop sample Mu 823—same as above (see text fig. 2 for locations).

DIAGNOSIS. *Skylonia* with spindles with eight to eleven zooecia per longitudinal row, the zooecia rectangular in outline, apertures circular or higher than wide, frontal pores only in terminal zooecia of lateral rows.

DESCRIPTION. The length and width of the few complete spindles vary from 1·0 mm long by 0·31 mm wide to 1·27 mm long by 0·35 mm wide. The spindles reach their maximum diameter at or just below the middle. Each longitudinal row consists of eight to eleven zooecia of a rectangular shape. The width of the zooecia varies between 0·29 and 0·38 mm, but most are between 0·32 and 0·34 mm wide. The width/length ratio of the median zooecia varies between 1·3 and 2·1 mm. Only the terminal zooecia of the lateral rows carry proximal frontal pores. The apertures are circular or somewhat higher than wide. In some well-preserved specimens the proximal side of the aperture is slightly sinuous (Pl. 1, figs. 11a and 12). The apertures are situated in the centre of a generally low elevation. The width of the aperture of the median zooecia varies from 0·04 to 0·07 mm. The apertures above the spindle's greatest diameter open obliquely upwards. The distal end of the frontal cover is depressed, forming a shallow groove. Only rarely two low, lateral knobs flank the aperture.

Each zooecium is connected with each of the surrounding ones by means of a minute communication-pore.

REMARKS. *Skylonia sandbergi* n. sp. differs from *S. mirabilis* Thomas in the shape of the zooecia, which are rectangular and not hexagonal, and in the shape of the aperture. *S. sandbergi* differs from *S. dohmi* (Sandberg) and *S. thomasi* n. sp. in the absence of a well-developed elliptical raised rim round the apertures, and of well-developed knobs flanking the aperture and in the smaller number of zooecia in each longitudinal row.

Skylonia sarawakensis n. sp.

(Pl. 3, figs. 1–7)

NAME. After the State of Sarawak, Malaysian Borneo.

TYPE LOCALITY. Tanjong (Cape) Semilajau (sample Bu 509), Sarawak.

TYPE STRATUM. Nyalau Formation of Early Miocene age (*Globorotalia kugleri* zone).

HOLOTYPE. Spindle (D 51501).

PARATYPES. One hundred and seventy specimens (D 51502–51664 and RGM 172541–172544) all collected from the Nyalau Formation at Sungei (River) Sut

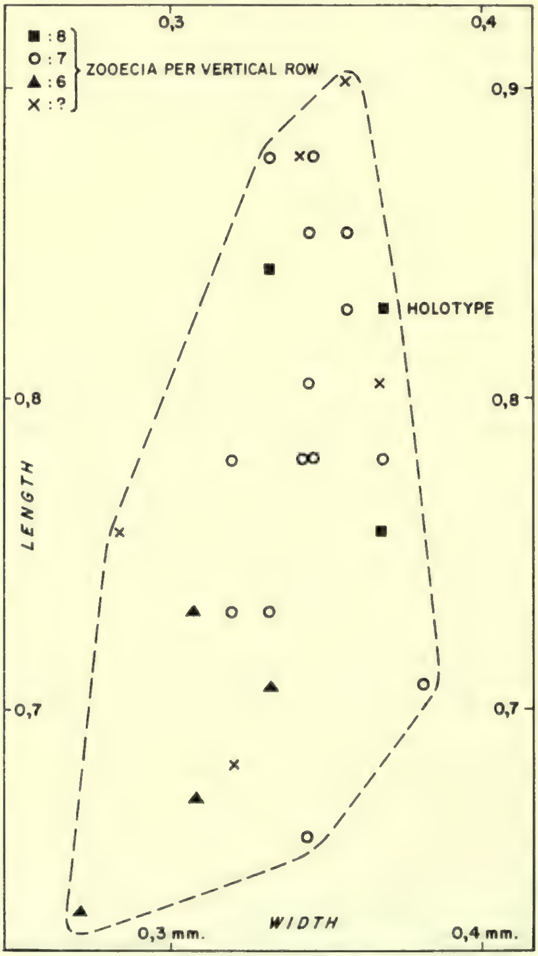

FIG. 3. Length and width measurements on *Skylonia sarawakensis* n. sp.

(samples Ca 53 and 54), Sungei Selungun (sample R 434), Sungei Perihas (samples R 860 and 861) and Sungei Sigrok (sample B 159) and Suai well 5 (4790–4800 ft depth), Sarawak (see text fig. 2).

DIAGNOSIS. *Skylonia* with spindles rather thick-set, with six to eight zooecia in each longitudinal row and with apertures of zooecia on the widest part of the spindle with two conspicuous and smooth flanking knobs.

DESCRIPTION. The shape of the spindles is variable, the maximum width is at the middle or above it. A number of spindles were measured and the result plotted in text fig. 3. Most of the spindles are slightly damaged or worn at their ends and the measured length is always slightly less than the original one.

Each longitudinal row consists of six to eight zooecia. The terminal zooecia are higher than wide, the others much wider than high. Their shape is rectangular or hexagonal, the proximal and distal boundaries being long and straight, the lateral ones straight or slightly zig-zag. The maximum width of the zooecium is 0·22 mm and the maximum height 0·13 mm.

The shape of the aperture changes from higher than wide (0·07 mm) at the proximal end, through circular to horizontal and slit-like (0·03 to 0·06 mm wide) in the middle of the spindle and back to somewhat higher than wide at the distal end.

A well-developed and thick rim is present round the apertures of all zooecia except that of the initial one. Three or four zooecia near the middle of the spindle have two large, smooth knobs flanking the slit-like aperture. The two preceding and the two succeeding zooecia feature only weakly developed knobs.

Frontal pores are present in this species (Pl. 3, fig. 2), but due to the bad preservation, only one good example was found in a proximal zooecium of a lateral row. In several specimens no such pore was observed in the frontal row.

Skylonia thomasi n. sp.

NAME. In honour of the late Dr H. D. Thomas.

DIAGNOSIS. *Skylonia* with spindles with more than ten zooecia in each longitudinal row, the apertures transversely elongate and with a low raised rim or two flanking knobs, proximal and distal zooecial boundaries slightly curved towards the distal end and with proximal frontal pores in the terminal zooecia of the lateral rows only.

REMARKS. Two forms were found, one in sediments of Late Tertiary *f* age or Middle Miocene, on Madura (Indonesia), the other in sediments of Tertiary *g* or Late Miocene age in Sabah (Malaysian Borneo). They are treated here as two subspecies as they differ only in subordinate characters.

Three fragments of a stout form were collected from Uppermost Miocene or Lowermost Pliocene (i.e. *Globorotalia margaritae* zone) beds in well Lamu-2 (596–600 ft depth) in Kenya (RGM 172545). In the shape of the frontal plate and the raised rim these fragments show affinity with *Skylonia thomasi* n. sp., but complete spindles are needed for a full evaluation. The maximum width of these fragments varies between 0·44 and 0·46 mm, the maximum width of the zooecium is 0·29 mm and its height 0·15 mm. The maximum width of the aperture is 0·07 to 0·09 mm.

Another fragment with wide open zooecia (Pl. 4, fig. 7) was found in a sample from the Thuvu sediment Group of Late Miocene age (*Globorotalia margaritae* zone, lower part) at the southeast coast of Vitu Levu, Fiji Islands (RGM 172546). Here again an affinity with *Skylonia thomasi* n. sp. is assumed. *S. thomasi* somewhat resembles *S. dohmi* (Sandberg) in the outline of the spindle and in the configuration of the raised rim. It differs in having frontal pores in the lateral rows only and not in all four rows as in *S. dohmi,* which lacks the flanking knobs of the apertures and has a slightly higher number of zooecia per vertical row.

Skylonia thomasi thomasi n. sp. *et* n. subsp.

(Pl. 4, figs. 1–4)

TYPE LOCALITY. Outcrop at N 5°13′–E 119°04′07″ (sample Jo 121), Dent Peninsula, Sabah, Malaysian Borneo.

TYPE STRATUM. Sebahat Formation of Late Miocene age (Tertiary *g*).

HOLOTYPE. Spindle D 51665.

PARATYPES. Thirty-four spindles or fragments (D 51666–51698 and RGM 172547).

DISTRIBUTION. Only in the Sebahat Formation at the type locality and at N 5°13′03″–E 119°04′02″ (sample Mt 2196).

DIAGNOSIS. *Skylonia thomasi* with spindles widest below the middle, with eleven to thirteen zooecia in each longitudinal row and a straight proximal end with the initial zooecium in the same plane as the succeeding zooecia of the frontal row.

DESCRIPTION. The spindles are approximately 1·5 mm long and 0·37 mm wide with their maximum width below the middle.

The initial zooecium has a relatively large aperture of 0·07 mm high and 0·04 mm wide, which is surrounded by a low rim. The shape of the apertures changes from circular to transversely elongate (0·04 mm wide) in the middle part of the spindles. The raised rim is either low and rounded or developed as two small smooth knobs flanking the apertures (Pl. 4, fig. 4). A groove de-limits the elliptical outer edge of the raised rim.

The shape of the zooecia changes from higher than wide at both ends to much wider than high (0·23 to 0·24 mm wide by 0·11 mm high) in the middle part of the spindle. The proximal and distal margins of the zooecia are somewhat curved.

In the very few complete spindles available, it was observed that the longitudinal rows contain eleven to thirteen zooecia. Only the proximal and distal zooecia of the lateral rows show a small circular frontal pore at their proximal end.

Each zooecium is connected with the surrounding six zooecia by a minute communication-pore (Pl. 4, fig. 2).

Remarks. This subspecies differs from the slightly older subspecies *Skylonia thomasi madurensis* n. subsp. in the shape of the spindles and in the shape of the proximal end.

Skylonia thomasi madurensis n. sp. *et* n. subsp.

(Pl. 4, figs. 5–7)

Name. After the Island of Madura, Indonesia.

Type locality. Kali (river) Ambunten (sample Be 1421), approx. 3 km SSE of Ambunten village, East Madura.

Type stratum. Sediments of Tertiary f_3 age or Middle Miocene.

Holotype. Spindle D 51699.

Paratypes. Four spindles and one fragment (D 51700–51705).

Distribution. A single specimen from ditch-cuttings of Cochrane well 1 (4140–4150 ft depth), off-shore Sarawak and of supposedly Middle Miocene age, very probably also belongs to this subspecies.

Diagnosis. *Skylonia thomasi* with spindles long and narrow with sides nearly parallel, the proximal end curved forward, the initial zooecium making an angle with the succeeding zooecia of the frontal row.

Description. The spindles are long (more than 1·5 mm) and narrow with the proximal end curved forward, causing the initial zooecium to make an angle of approximately 45° with the axis of the spindle. Their maximum width is 0·37 mm.

The number of zooecia per vertical row is unknown but is definitely more than eleven. The maximum width of the zooecia in the median part of the spindle is 0·23 mm and their height 0·13 mm. In the terminal zooecia a raised rim is present round the apertures. In the middle part of the spindles it is well developed and elliptical in shape, often with two smooth knobs flanking the apertures. The distal end of the raised rim merges in a depression which is probably ornamented with a number of low vertical ridges. The shape of the aperture is difficult to determine with certainty due to the mediocre preservation of the material, but the usual change from vertically elongate through circular to transversely elongate was observed. The outline of the zooecia is rectangular with slightly curved proximal and distal boundaries.

Proximal frontal pores were observed in the end zooecia of the lateral rows only.

Skylonia sp. A

(Pl. 3, fig. 8)

Remarks. Two fragments of a species with rectangular unornamented zooecia were found in the Klasaman Formation at Waileh on Salawati Island, opposite the west end of Bird's Head Peninsula, New Guinea. The age is Late Miocene or Pliocene. One fragment is badly corroded, the other is smaller and well preserved.

It shows that the zooecia are rectangular and slightly convex and the central openings are transversely rectangular. These fragments probably belong to a new species but more material is needed to define it properly.

Three very badly preserved fragments, probably belonging to the same species, occurred in a sample of the Berili Marl, at approx. 4 km ESE of Aloguinsan on Cebu Island, Philippines. Their age is Late Miocene.

The material is stored under numbers D 51496–51500.

Skylonia sp. B

(Pl. 3, fig. 9)

REMARKS. A single fragment of a rather well-preserved specimen from the Lower Miocene Chipola Formation at Fairley Creek in Florida (sample T.U. 823), and a heavily decalcified fragment from the same formation at Chipola River (sample T.U. 548) was obtained for study through the courtesy of Dr R. J. Scolaro. The well-preserved fragment is 0·73 mm long and comprises three or four zooecia per vertical row. The proximal end is broken off, but two of the zooecia of opposite rows are apparently the first lateral zooecia as two frontal pores are present. The fragment belonged to a still functional spindle, as the opesiae have not been covered yet by the calcified frontal plates with their small central openings. The openings change in shape from vertically elongate (0·06 to 0·07 mm wide and 0·10 mm high) to circular with a diameter of 0·10 mm. The fragment T.U. 548 shows that the openings ultimately become small and nearly circular.

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This paper was intended to precede a second contribution by the author, dealing with related Eocene and Oligocene skyloniid genera, but owing to unforeseen delays the order of publication was reversed. The reader is referred to KEIJ, A. J. 1972. *Sylonika* and *Kylonisa*, two new Palaeogene bryozoan genera (Cheilostomata, Skyloniidae). *Scripta Geol.* **11**: 1–15.

A. J. KEIJ
c/o SHELL INTERNATIONALE PETROLEUM
MAATSCHAPPIJ B.V.
POSTBUS 162
THE HAGUE
NETHERLANDS

PLATE 1

Planicellaria fenestrata d'Orbigny

FIG. 1. Part of internode with three occluded zooecia. Lower Thanetian of Musitu, Spain. ×18.

Vincularia fragilis (Defrance)

FIG. 2. Two zooecia with abnormally deep-lying calcareous closures; normal, flush closures usually show opercular scars. Lower Lutetian of Nalinnes, Belgium. ×35.

Stamenocella oculata (Ulrich & Bassler)

FIG. 3. Proximal end of internode with large initial zooecium which remained uncalcified in contrast to the succeeding zooecia which have nearly complete frontal closures. Note presence of opercular scars. Paleocene Vincentown Marl at Rancocas Creek, Burlington County, New Jersey, U.S.A. ×18.

" Smittipora " sp.

FIG. 4. Proximal end with small calcified initial zooecium with minute central pore. Ypresian of marlpit of Sourbet, Horsarrieu near St Sever (Landes), France. ×18.

" Cellaria " mucronata Meunier & Pergens

FIG. 5. Proximal end with large anascaform initial zooecium completely open. Montian Calcaire de Mons in boring Obourg (depth 56 m) near Mons, Belgium. ×18.

Vibracella (Discovibracella) oculata Voigt

FIG. 6. Few of the zooecia are calcified, leaving a slit-like opening. Opercular scars present. Montian Calcaire de Mons in boring Obourg (depth 56 m) near Mons, Belgium. ×18.

Nellia tenuis Harmer

FIG. 7. Proximal end with calcified initial zooecium. Recent, South China Sea at N 5°59′–E 112°35′ at 430 m depth. ×35.

Scrupocellaria milneri Canu & Bassler

FIG. 8. Two of the figured zooecia are calcified, the third one not. Oligocene Byram Marl of type locality at Byram station, 7 miles north of Jackson, Mississippi, U.S.A. ×35.

Encicellaria hofkeri Keij

FIG. 9. Incomplete spindle with initial zooecium and two succeeding zooecia occluded and remainder of zooecia open. Maastrichtian Maastricht Limestone in ENCI quarry near Maastricht, Netherlands. ×18.

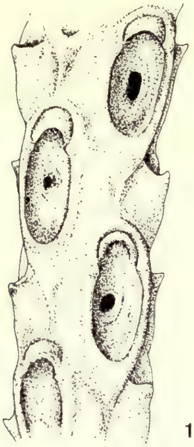
Skylonia sandbergi n. sp.

FIG. 10. Middle part of spindle. Lower Miocene, Engkabang well 1 (3580–3590 ft depth), Sarawak. ×35.

FIG. 11. (a) Complete spindle from the side and (b) proximal end seen from the front with its large initial zooecium. Lower Miocene of Cochrane well 1 (7510–7520 ft depth), off-shore Sarawak in South China Sea. Holotype. ×35.

FIG. 12. Part of spindle. Same well and age at 5370–5380 ft depth. ×35.

FIG. 13. Distal half of spindle with the zooecia not closed with calcified lamellae. Lower Miocene of Suai well 1 (core of 1897–1903 ft depth), Sarawak. ×35.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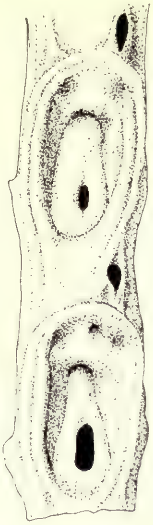
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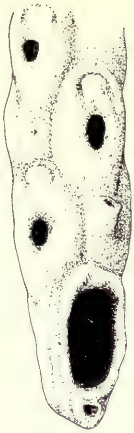
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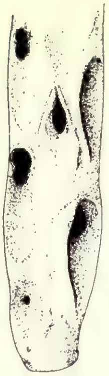
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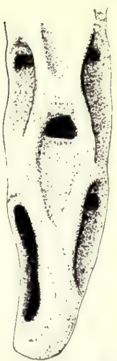
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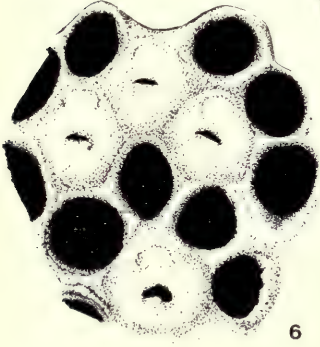
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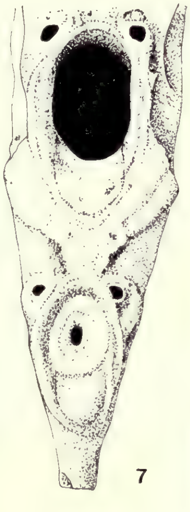
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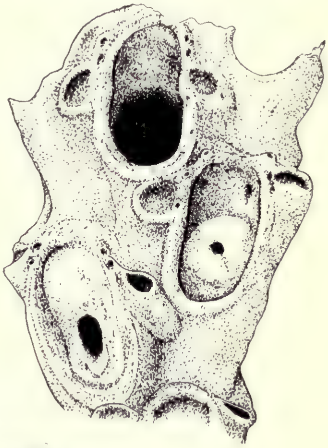
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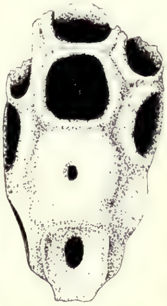
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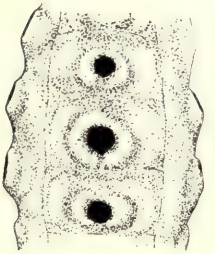
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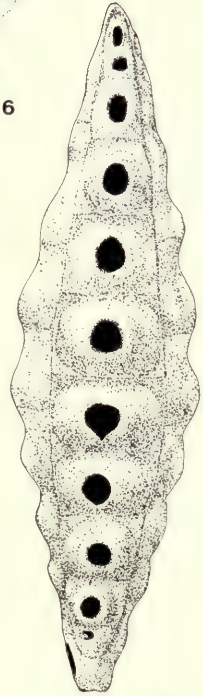
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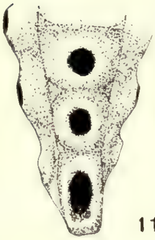
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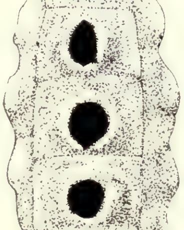
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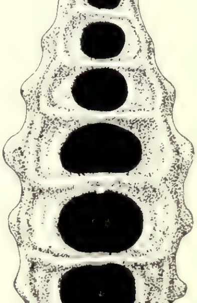
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PLATE 2

Skylonia bermudezi n. sp.

FIG. 1. Nearly complete spindle with calcified zooecia and three frontal pores in the proximal and distal zooecia. ×35.

FIG. 2. Spindle with the frontal closure not yet at full extension. ×35.

FIG. 3. Large, incomplete spindle with frontal closures and small central openings (Holotype). ×35.

Upper Eocene Jabaco Formation of Jabaco (loc. Bermudez B 337A), Cuba.

FIG. 4. Badly preserved spindle which probably belongs to this species. Middle Eocene Lower Guayabal Formation of Chumatlan River, Mexico. ×35.

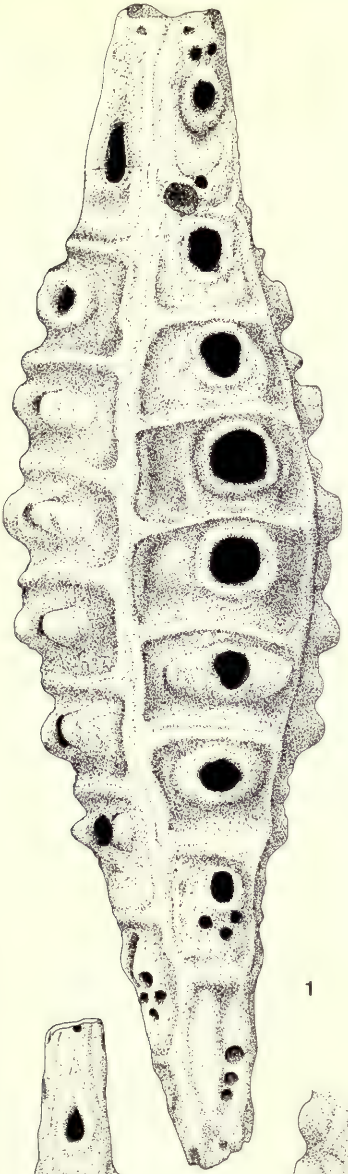
Skylonia dohmi (Sandberg)

FIGS. 5–7. 5. Distal end of spindle showing presence of single frontal pores in distal zooecia.

6. Middle part of spindle with low knob-like protrusions flanking the slit-like central openings.

7. Proximal end of spindle from the side showing presence of single frontal pores in proximal zooecia.

Lower Miocene Baitoa Formation of Dominican Republic. ×35.



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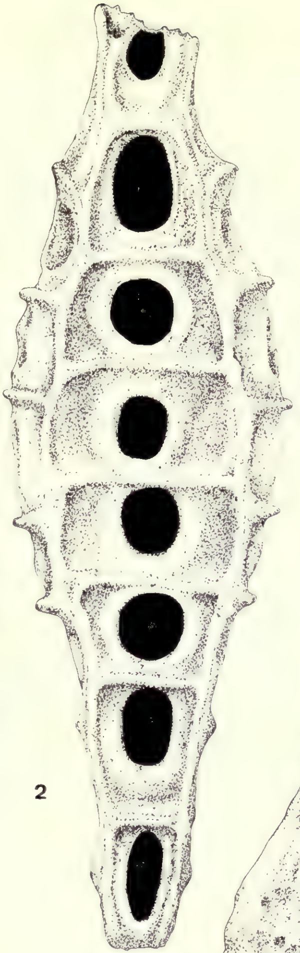

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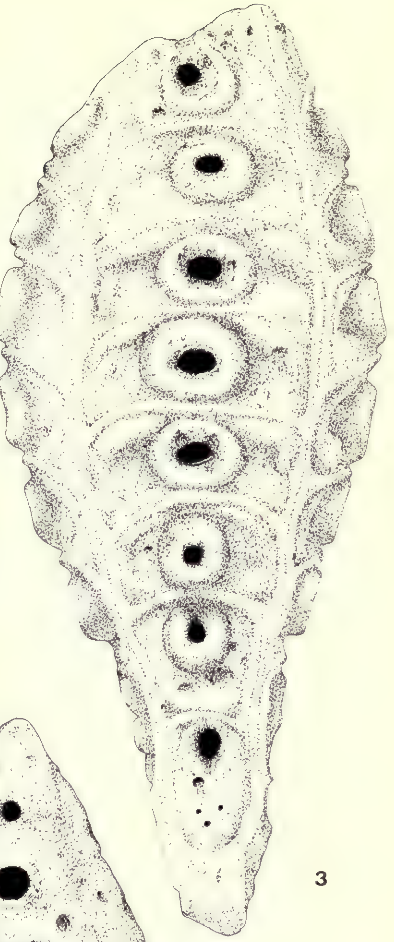

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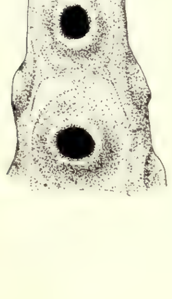

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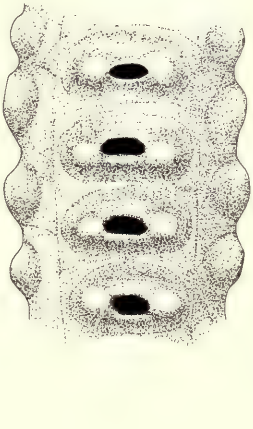

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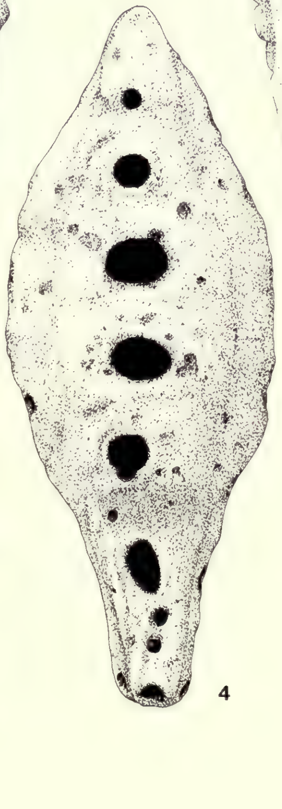

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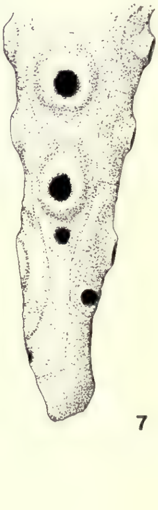

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PLATE 4

Skylonia thomasi thomasi n. sp. *et* n. subsp.

FIG. 1. (a) Complete spindle from the side, (b) proximal end of spindle, (c) proximal part of spindle with initial zooecium, (d) distal end of spindle. Holotype.

FIG. 2. Distal end of fragment of spindle showing pores between zooecia in all four rows.

FIG. 3. Fragment of spindle without frontal closures.

FIG. 4. Middle part of spindle in which low knobs flank the elliptical central opening.

Upper Miocene Sebahat Formation, Dent Peninsula, Sabah. ×35.

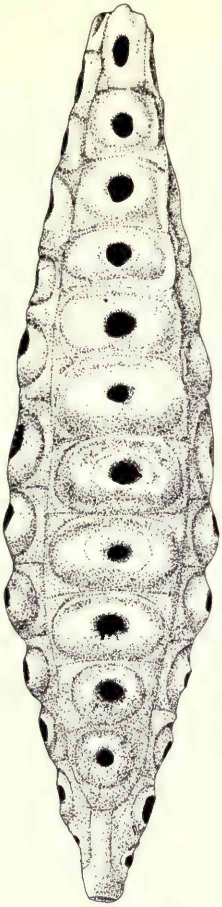
Skylonia thomasi madurensis n. sp. *et* n. subsp.

FIG. 5. (a) Nearly complete spindle from the side, (b) proximal end, (c) proximal part with initial zooecium, (d) proximal part from the side. Holotype.

FIG. 6. Proximal end of spindle lacking frontal closures of the zooecia.

Middle Miocene of Kali Ambunten, Eastern Madura, Indonesia. ×35.

FIG. 7. Fragment of spindle found in Upper Miocene Thuvu Group of Viti Levu, Fiji Islands. ×35.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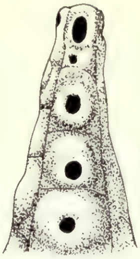
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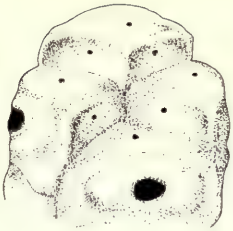
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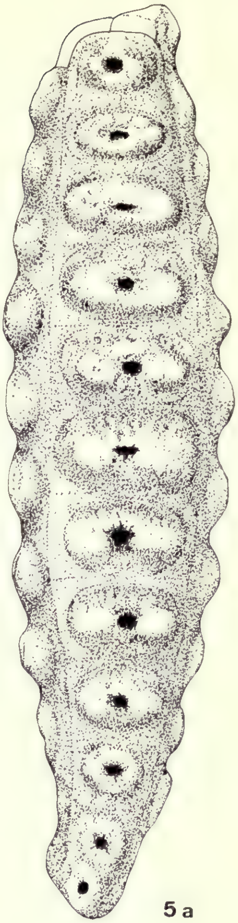
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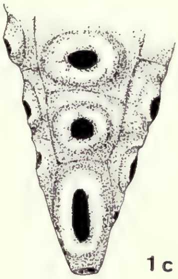
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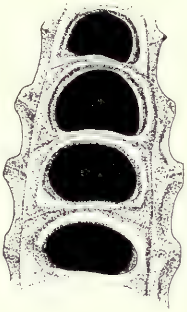
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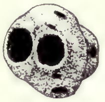
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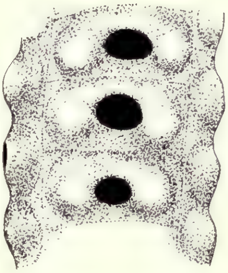
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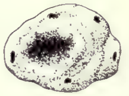
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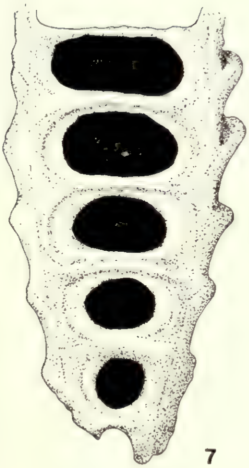
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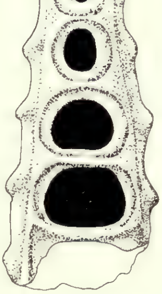
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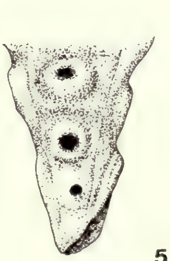
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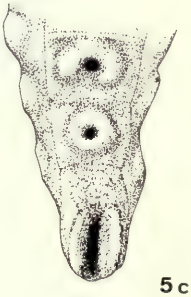
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M. K. HOWARTH

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 24 No. 4
LONDON: 1973

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BY

M. K. HOWARTH

Pp. 235–277; 9 *Plates,* 5 *Text-figures*

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By M. K. HOWARTH

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SYNOPSIS

The Grey Shales is the lowest formation of the Upper Lias in Yorkshire, and is the type section of most of the Tenuicostatum Zone, the lowest zone of the Toarcian. The formation, consisting of 13·5 m of grey shale containing 15 rows of calcareous nodules, is described in detail, and there are geological maps of the two main outcrops. The Hildoceratid ammonite *Protogrammoceras paltum* (Buckman) occurs near the base of the formation, and a rich fauna of Dactylioceratidae occurs in the upper 10 m, which has been divided into four species of *Dactylioceras* (*Orthodactylites*), including the new species *D.* (*O.*) *clevelandicum*. These ammonites form the basis of the following newly-proposed scheme of subzones :

Tenuicostatum Zone {
Subzone of *Dactylioceras* (*O.*) *semicelatum*
Subzone of *D.* (*O.*) *tenuicostatum*
Subzone of *D.* (*O.*) *clevelandicum*
Subzone of *Protogrammoceras paltum*

A single example of *D.* (*Dactylioceras*) *pseudocommune* Fucini found in north-west Cleveland is also described, and is the earliest Dactylioceratid known in Britain. Correlations are made with all other areas of the world from which beds containing Tenuicostatum Zone ammonites have been described.

The preservation of the Grey Shales species of *Dactylioceras*, with the shell intact or as internal moulds, is complicated by the unique shell structure of Dactylioceratidae, in which a complete inner shell is formed. Four basically different appearances of the ribbing of the Yorkshire species are described.

I. INTRODUCTION

DETAILED descriptions of the stratigraphy and ammonite fauna of most of the Middle and Upper Lias of the Yorkshire coast have appeared in recent years. Only the Grey Shale " Series " (here called the Grey Shales) remains undescribed. It is the basal lithological division of the Upper Lias, overlying the Middle Lias Ironstone " Series " (Howarth 1955), and is overlain by the Jet Rock and Alum Shale "Series" (Howarth 1962), and then by higher beds at Ravenscar up to the top of the Lias (Dean 1954). With this description of the Grey Shales, the full succession is now complete from the base of the Middle Lias up to the top of the Upper Lias. The Yorkshire coast is the type area for many of the zones and subzones of the Middle and Upper Lias, and the Grey Shales make up most of the thickness of the Tenuicostatum Zone, the basal zone of the Toarcian or Upper Lias. It is the type area of both the Tenuicostatum Zone and the Toarcian Stage. The rich Dacylioceratidae ammonite fauna of the Grey Shales has enabled the Tenuicostatum Zone to be divided into subzones for the first time, on the basis of a thick, expanded succession. The discovery at the top of the Grey Shales of a rich *Tiltoniceras* fauna, previously known only from the Transition Bed of the English Midlands, shows for the first time that this ammonite occurs at the top of the Tenuicostatum Zone.

There is no satisfactory previous account of the stratigraphical succession within the Grey Shales of Yorkshire. Tate & Blake's (1876 : 168–172) general description of the lithology and occurrence of fossils is good, but neither of their two detailed sections is an adequate description of the constant succession of shales and doggers that occurs in the coastal exposures. No further description or details of the succession were given by Fox-Strangways & Barrow (1915 : 16) or by Buckman (1915*a* : 76) in the same work. A collection of 42 ammonites from the Grey Shales was made by Dr L. R. Cox in 1929, together with a bed by bed succession that can be identified with the sequence described here, and these ammonites are included in this description. Some work on the Grey Shales was done by Professor Sylvester-Bradley in the mid-1950s but has never been published. The bed numbers 1–32 were given by him in a manuscript account of the stratigraphical succession, and it was because of this account, which he kindly communicated to me, that the Cannon Ball Doggers immediately overlying the Grey Shales were given the bed number 33 (Howarth 1962 : 388). The only previous allusion to the stratigraphical sequence within the Tenuicostatum Zone was the four horizons listed by Dean, Donovan & Howarth (1961 : 476), also taken from Professor Sylvester-Bradley's manuscript account.

All the Grey Shales localities on the coast are foreshore reefs, and as the beds are less resistant than most other parts of the Middle and Upper Lias, they form some of the lowest reefs occurring almost wholly between " mid-tide " and low water mark. The reefs are flat wave-cut platforms sloping seawards at a very low angle, and the amount exposed differs greatly according to the type of tide. For this reason all the localities were visited at low water of spring tides. Geological maps were drawn for each locality on a scale of 1 : 2,500, the base maps used being the 1928 edition of the Ordnance Survey (the latest available), and on those reproduced here as Text-figs. 2 and 3 the lines drawn as " low water mark " are those of fairly low spring tides. Considerably less is seen at low water of ordinary tides, and at neap tides exposures are even more restricted. Help in the correct alignment of the faults and some key beds shown on both maps was obtained from aerial photographs taken by Dr J. K. St. Joseph of Cambridge University, to whom thanks are due.

Most of the localities showing exposures of Grey Shales on the north-western escarpment of the Cleveland Hills between Saltburn and Osmotherley were also visited, mainly in order to examine the lowest beds. The succession was found to be no different from that on the coast, and it is only in the top few beds of the Ironstone " Series " that a different development occurs, with one of the beds containing a highly significant specimen of *Dactylioceras*.

II. STRATIGRAPHICAL SUCCESSION

The Grey Shales consists of 13·56 m (44 ft 6 in.) of grey shale, containing 15 rows of nodules or doggers of calcareous, and sometimes sideritic, argillaceous limestone. Pyritization occurs in some doggers and there are granular masses of pyrite in the upper shale beds. The doggers are distinctive and constant in all the exposures, and some of the rows form striking features. Thus bed 3 is a continuous bed of sideritic calcified mudstone which weathers red in patches, the Six Red Nodule beds (beds 7–17) occur as closely spaced rows of dark red nodules on many of the reefs, and beds 28 and 30 form long lines of frequent doggers prominent at all localities. Ammonites are abundant in the upper 9·80 m (32 ft) of the Grey Shales, and a collection of 560 well-preserved Dactylioceratidae was obtained from the nodules of beds 18, 19, 20, 22, 24, 28 and 30. A further 450 ammonites, mainly *Tiltoniceras*, were obtained from the shell beds in bed 32. The lower 3·76 m (12 ft 6 in.) contain very few ammonites, in fact only rare specimens have been found in beds 2 and 3, and there are none at all in beds 1 and 4–17. Belemnites are common at almost all horizons in the Grey Shales, including those that do not contain ammonites. Other faunal elements are much less common, and the bivalves and gastropods in the long list given by Tate & Blake (1876 : 172) are only rarely found at most horizons. An exception is "*Posidonia*" *radiata* (Goldfuss), and perhaps other related species, which is abundant in shell beds in bed 32 and common at other horizons.

The upper limit of the Grey Shales and also of the Tenuicostatum Zone is now placed at the top of bed 32 and not at the bottom of bed 32 as previously (Howarth 1962 : 388), following the discovery of many crushed *Dactylioceras semicelatum* throughout that bed. It was also realized that the commonest ammonite in bed 32, especially in two shell beds at the base, is *Tiltoniceras antiquum* (Wright) and not *Eleganticeras elegantulum* (Young & Bird) as recorded previously (Howarth 1962 : 388). Both *Dactylioceras semicelatum* and *Tiltoniceras* are traditionally ammonites of the Tenuicostatum Zone, and so the top boundary of the zone has to be placed at the top of bed 32. The top of the Grey Shales is placed at the same position because the shales of bed 32 are similar to those of the beds below, and real bituminous shales start in bed 34 immediately above the Cannon Ball Doggers at the base of the Jet Rock.

The lower limit of the Grey Shales is at the base of bed 1, immediately above the top bed of the Ironstone " Series " (Kettleness bed 28). The position of the base of the Tenuicostatum Zone is a complicated question involving lithological and palaeontological correlations and is fully discussed later (p. 267).

The following detailed succession is constant for all the localities at which the Grey Shales are exposed, for the lithology shows no variation and the thickness shows very little variation. The thicknesses were, in fact, measured in vertical cliff sections as follows : beds 1–18 at Brackenberry Wyke, Runswick Bay, west and east Kettleness, and Hawsker Bottoms ; beds 18–32 at east Kettleness ; beds 22–32 at Loop Wyke and Hawsker Bottoms ; and beds 28–32 at Brackenberry Wyke. The beds of nodules are of constant thickness, while shale beds may vary by up to 25% between thickest and thinnest, but usually the variation is considerably less. Fossil records are included from all the exposures, numbers prefixed by " C." being the register numbers of specimens in the collections of the British Museum (Natural History), while the first prefix letter *a* to *k* indicates the locality from which the specimen came as listed on pp. 242–244.

Bed no.		m	(ft in.)
33	The Cannon Ball Doggers. Basal bed of the Jet Rock, Exaratum Subzone. *Eleganticeras elegantulum* (Young & Bird) . . .	0·15	(0 6)

Zone of *Dactylioceras tenuicostatum*
Subzone of *Dactylioceras semicelatum*

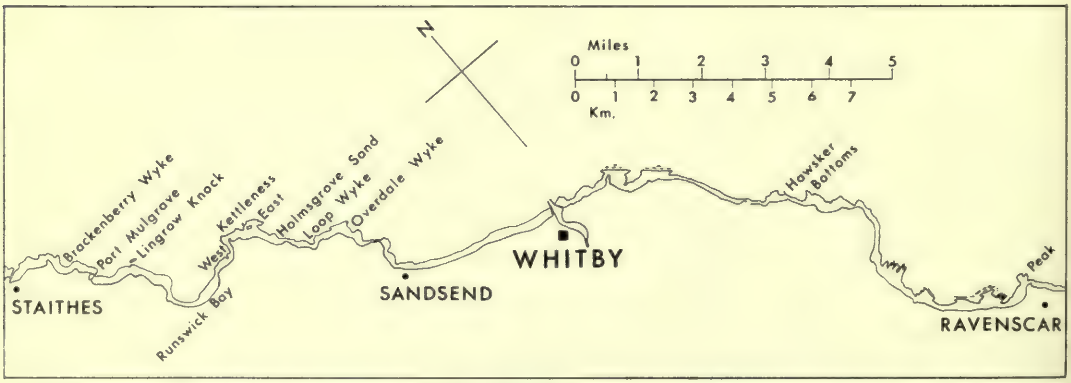
The Grey Shales. Total thickness 13·56 m (44 ft 6 in.)

Bed no.		m	(ft in.)
32	Shale, grey, bituminous in places, with occasional flat calcareous nodules near top, constant and widespread shell-beds at base and 0·10 m above base, and occasional shell-beds throughout. Basal two shell-beds contain large numbers of crushed *Tiltoniceras antiquum* (*b* C.50407–12, C.77349–59 ; *f* C.77364 ; *h* C.77361–63), *Dactylioceras semicelatum* (*b* C.47941, C.77360 ; *f* C.77365 ; *g* C.77366) and "*Posidonia*" *radiata* (Goldfuss). The same species occur less abundantly in shell-beds up to 0·30 m below top—*T. antiquum* (*k* C.77369), *D. semicelatum* (*j* C.77367, 68 ; *k* C.77369–74)	1·83	(6 0)
31	Shale, grey. Crushed *Dactylioceras semicelatum* throughout, some in shell-beds, but especially common near middle of bed (*b* C.77343, 44 ; *c* C.47932 ; *f* C.77341, 42 ; *g* C.77340 ; *j* C.77345–48) . . .	2·13	(7 0)
30	Large, very hard, calcareous doggers, with much pyritization, average size 0·15 m × 0·20 m × 0·10 m thick. *Dactylioceras semicelatum* common, usually horizontal through middle of doggers, occasionally at varying angles (*b* C.47955, 56, C.77318–26 ; *c* C.47931, 33, 34, C.77327, 28 ; *f* C.77297–314 ; *g* C.77315, 16 ; *h* C.77329–32 ; *j* C.77333–39 ; *k* C.77317)	0·10	(0 4)
29	Shale, grey, granular pyrites common, especially in lower half. Occasional crushed *Dactylioceras semicelatum*	1·07	(3 6)
28	Large, hard, calcareous doggers, in two adjacent rows ; less pyrite than in doggers of bed 30, and individual doggers rather smaller, average size 0·12 m × 0·15 m × 0·08 m thick, but upper row larger than lower row. Knots of pyrites in shale between doggers. *Dactylioceras semicelatum* in some doggers (*b* C.47940, 46, 53, 54,		

Bed no.		m	(ft	in.)
	C.77276–78, C.77283, 84 ; *c* C.47936, 38, 39, 57, C.77269 ; *f* C.77270–75 ; *h* C.77285–94 ; *k* C.77279–82), large belemnites in others, also *Cenoceras astacoides* (Young & Bird) (*b* C.50414)	0·23	(0	9)
	Subzone of *Dactylioceras tenuicostatum*			
27	Shale, grey. Rare crushed specimens of *Dactylioceras tenuicostatum*	0·61	(2	0)
26	Thin calcareous nodules, flat and lens-shaped, weathering red. A few *Dactylioceras tenuicostatum* (*f* C.77257, 58 ; *g* C.77263–66 ; *h* C.77267, 68 ; *k* C.77259–61)	0·05	(0	2)
25	Shale, grey with occasional round calcareous nodules containing *Dactylioceras tenuicostatum*	0·61	(2	0)
24	Row of small spherical calcareous nodules, almost all with one *Dactylioceras tenuicostatum* lying horizontally through the middle (*b* C.47947, C.77225–56 ; *d* C.47923 ; *f* C.47926, 27, C.77187–215 ; *h* C.77220–24 ; *k* C.77216–19)	0·08	(0	3)
23	Shale, grey, occasional round calcareous nodules containing *Dactylioceras tenuicostatum*	0·38	(1	3)
22	Row of nodules as bed 24. *Dactylioceras tenuicostatum* (*b* C.47951, 52, C.77178–86 ; *c* C.47937, C.77159–69 ; *d* C.47912, 14–19, 24, 25 ; *f* C.77148–58 ; *g* C.50413, C.77170 ; *h* 77173–77 ; *k* C.77171, 72)	0·08	(0	3)
21	Shale, grey, occasional small calcareous nodules with *Dactylioceras tenuicostatum* (*d* C.47920–22)	0·76	(2	6)
20	Large scattered calcified lenses, weathering red ; each lens about 0·25 m across and 0·07 m thick, and occurring in two adjacent rows. *Dactylioceras tenuicostatum* (*b* C.77120–47 ; *f* C.77110–19 ; *g* C.77109)	0·15	(0	6)
	Subzone of *Dactylioceras clevelandicum*			
19	Shale, subdivided as follows :			
	19*c* Shale, grey	0·81	(2	8)
	19*b* Shale, grey, with scattered thin, flat, lens-shaped concretions, weathering red. Calcified clusters of *Dactylioceras clevelandicum* lying at all angles occur commonly between the red concretions (*a* C.50415–18, C.77077–84 ; *b* C.47944, 45, 48, C.76988, 89, C.77094–108 ; *c* C.77085–88 ; *d* C.77052–76 ; *e* C.77093 ; *f* C.76925–87 ; *g* C.50419–26, C.76990–77051 ; *k* C.77089–92)	0·05	(0	2)
	19*a* Shale, grey, basal 0·10 m closely laminated and bituminous, and weathers to form a step on foreshore reefs ; pale brown sandy masses 0·30 m above the base	0·41	(1	4)
18	Shale, grey, silty ; small calcareous nodules or calcified clusters of *Dactylioceras crosbeyi* lying at all angles occur in a row at the middle of the bed (*b* C.47950, C.76917–19 ; *c* C.76920 ; *d* C.47913, 42, 43 ; *e* C.76913–16 ; *f* C.76860–90 ; *g* C.76891–912 ; *k* C.76921–24)	0·38	(1	3)
	Subzone of *Protogrammoceras paltum*			
17	Sixth Red Nodules. Row of frequent grey calcareous and sideritic nodules, weathering deep red on the outside, average size 0·23 m × 0·15 m × 0·05–0·08 m thick. Some contain large belemnites and more rarely bivalves. No ammonites	0·08	(0	3)
16	Shale, grey	0·20	(0	8)
15	Fifth Red Nodules. As bed 17	0·08	(0	3)
14	Shale, grey	0·23	(0	9)
13	Fourth Red Nodules. As bed 17	0·05	(0	2)

Bed no.		m	(ft	in.)
12	Shale, grey	0·30	(1	0)
11	Third Red Nodules. As bed 17	0·05	(0	2)
10	Shale, grey	0·25	(0	10)
9	Second Red Nodules. As bed 17	0·05	(0	2)
8	Shale, grey	0·41	(1	4)
7	First Red Nodules. As bed 17	0·08	(0	3)
6	Shale, grey	0·53	(1	9)
5	Row of small, spherical, grey calcareous nodules. No ammonites	0·05	(0	2)
4	Shale, grey	0·36	(1	2)
3	Continuous bed of sideritic, calcareous mudstone, weathering red. Rare large specimens of *Protogrammoceras paltum* (*d* C.47972; *f* C.77296; *k* C.72521, C.77262), and crushed *Dactylioceras* sp. indet. (*f.* C.77295)	0·08	(0	3)
2	Shale, dark grey, closely laminated and bituminous; marked parting 0·20 m below top at some localities. Small calcareous nodule at base with impression of a *Lytoceras* sp. indet. (locality *f*)	0·53	(1	9)
1	Shale, grey	0·51	(1	8)
	THE IRONSTONE SERIES (see Howarth 1955 : 156—bed numbers of Kettleness section)			
28	Row of frequent round calcareous nodules. Many *Pseudopecten aequivalvis* (J. Sowerby), and *Pholadomya ambigua* (J. Sowerby) in vertical life position	0·05	(0	2)
27	Shale, sandy	0·46	(1	6)
26	Shale, closely bedded, bituminous (= Sulphur Band)	0·15	(0	6)
	Zone of *Pleuroceras spinatum* Subzone of *Pleuroceras hawskerense*			
25	Shale, grey, sandy. Limestone nodules near base contain many *Pleuroceras hawskerense* (Young & Bird)	0·33	(1	1)

DETAILS OF LOCALITIES (Text-fig. 1)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Miles
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3
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7
Km.
Brackenberry Wyke
Port Mulgrave
Lingrow Knock
Kettleness
West
East
Holmsgrove Sand
Loop Wyke
Overdale Wyke
Howsker Bottoms
Peak
STAITHES
Runswick Bay
SANDSEND
WHITBY
RAVENSCAR

FIG. 1. Localities of exposures of Grey Shales on the foreshore of the north Yorkshire coast.

a. Brackenberry Wyke (see Text-fig. 2). The base of the Grey Shales first appears on the foreshore in Brackenberry Wyke at NZ 795185. Beds 3 and 5 follow, then

the Six Red Nodule beds form a striking feature running approximately north–south at NZ 796182. Beds 18 and 19 appear, but large boulders cover much of the upper half of bed 19 and bed 20. All the beds dip at a low angle to the east.

b. Port Mulgrave (see Text-fig. 2). The last exposure continues south-eastwards across Thorndale Shaft now clear of boulders, and all the beds are seen up to the top of the Grey Shales. A north–south double fault crosses the reef at NZ 799179, and with an upthrow of about 5 m (16·5 ft) to the east, most of the Grey Shales are repeated again on the eastern side of the fault. The lowest bed seen at low water of spring tides is the First Red Nodules, bed 7, then higher beds follow southwards up to beds 30 and 31 which abut the north pier of Port Mulgrave (NZ 800177). Immediately south of the south pier beds 19–32 appear again on foreshore reefs, and beds 31 and 32 occupy the seaward half of the reef across the whole of Rosedale Wyke eastwards to Lingrow Knock (see Howarth 1962 : pl. 26).

The whole of the outcrop starting in Brackenberry Wyke and ending in Rosedale Wyke is well exposed and forms a good collecting ground.

c. Lingrow Knock. The Runswick Bay Fault, consisting here of two parallel north–south faults about 8 m apart, crosses the reefs immediately west of Lingrow Knock (NZ 809173), and throws the beds up to the east by about 14 m (45 ft) (Howarth 1962 : pl. 26). The whole of the Grey Shales occupies the reef east of the fault, the strike of the beds now being east–west with a slight dip to the south. The lowest beds occur at low water mark and the highest at the base of the cliff, but beds 5–7 are missing, cut out by a small fault. The detached reef of Lingrow Knock (which is easily accessible at low spring tides) consists largely of the top ironstone of the Ironstone Series (Kettleness bed 24, Howarth 1955 : 156). The nodules of bed 28 and then the base of the Grey Shales occur farther south on the seaward edge of the main reef. This exposure is covered by boulders at its south-eastern end.

d. Runswick Bay. Apart from a small exposure of beds 31 and 32 at the north end of Topman Steel (NZ 811168) north of Runswick, the next exposure of Grey Shales is the large reef occupying the south-eastern half of Runswick Bay. The strike is north–south and the dip to the west. The ironstone of Kettleness bed 24 occupies the eastern half of the reef, the base of the Grey Shales crosses the reef north–south at NZ 820155, then higher beds follow westwards up to bed 33 seen at the extreme western tip of the reef at NZ 815156. The Six Red Nodule beds and parts of beds 19 and 20 are well seen, but the remainder of the exposure is not good for collecting, being wet and largely covered with seaweed.

e. West Kettleness. The whole of the Grey Shales occurs on a small reef on the west side of Kettleness at NZ 829159. The beds strike north–south and dip at a low angle to the west, so the base is at the eastern end and the top at the western end of the reef. The lower half and the top beds are well seen, but beds 22 and 24 are difficult to trace.

f. East Kettleness (see Text-fig. 3). This large and structurally complicated exposure starts at NZ 836160, surrounds the hole in the reef known as Fillet Tail Dump, and extends to about NZ 839158 where boulders cover all but the seaward edge. The structure is a syncline dipping to the south at a low angle, so the base of the Grey Shales forms a semicircle round the west, north and east sides, and the top is at the base of the cliff to the south. Six or seven minor faults break up the semicircular continuity of the beds (Text-fig. 3). This is one of the best collecting localities for all horizons of the Grey Shales, which are very well exposed on the southern half, but wet and seaweed covered north and east of Fillet Tail Dump.

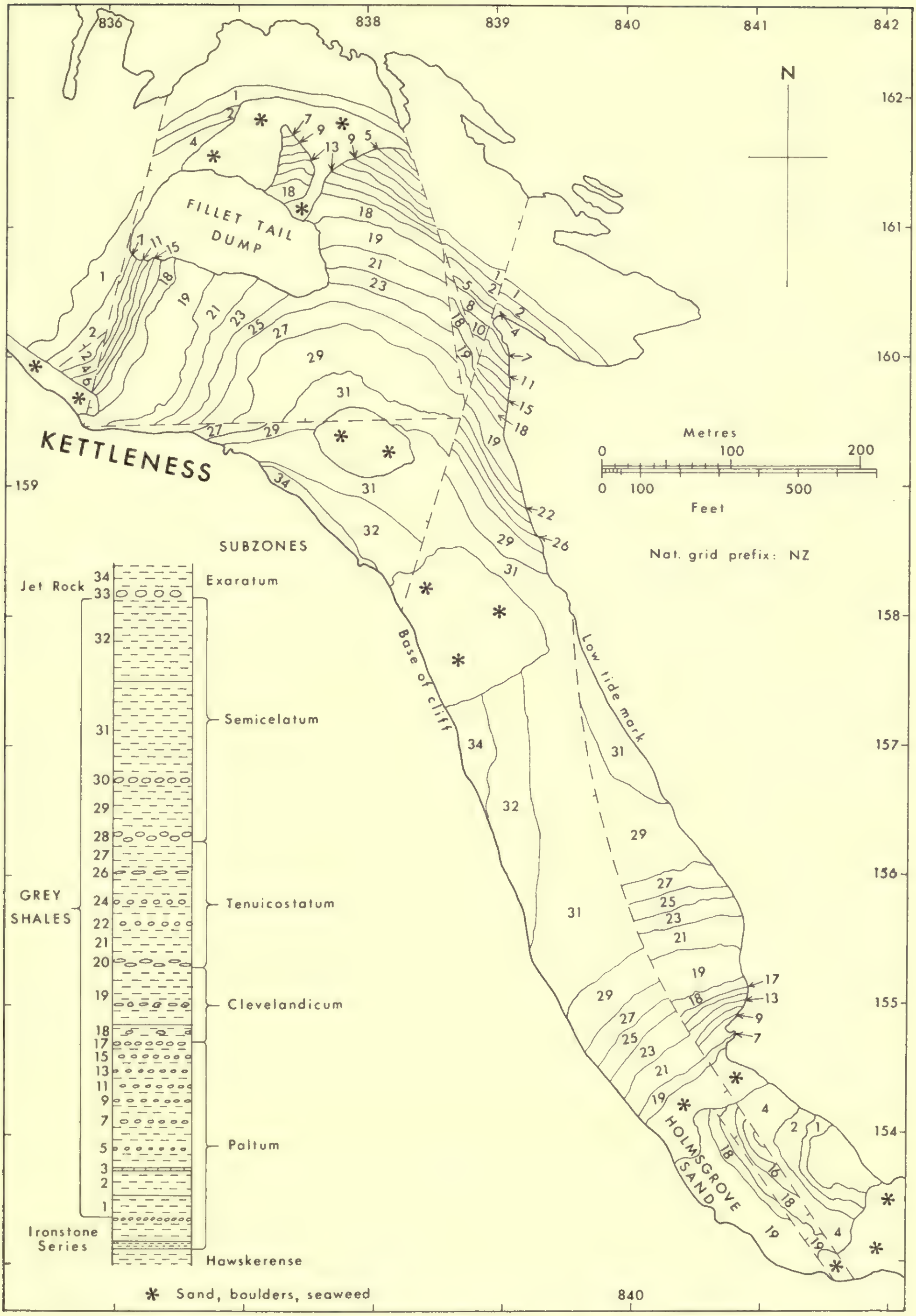
g. Holmsgrove Sand (see Text-fig. 3). The last exposure continues south-eastwards, now clear of boulders, to the cliff behind Holmsgrove Sand, until the foreshore is covered by a major cliff slump at NZ 842153. A north–west to south–east striking thrust fault cuts the reef into two parts, but all beds of the Grey Shales are exposed down to the two top beds of the Ironstone Series (beds 27 and 28) at NZ 842154. One of the best collections from bed 19*b* was made at this locality.

h. Loop Wyke. Small isolated reefs with beds 23–31 occur on the north side at NZ 845149. The main reef at NZ 848147 exposes beds from the middle of bed 21 (at low water of spring tides) up to the Jet Rock, and good collections were obtained from beds 28 and 30.

j. Overdale Wyke. Bed 33 runs east–west through the middle of Keldhowe Steel at NZ 855147, the top of the Grey Shales occurs to the south, and beds 29–31 occupy the whole of the reef in Overdale Wyke southwards as far as NZ 858142. The nodules of bed 30 form a large arcuate outcrop on the reef. Small outcrops of beds 31 and 32 occur under the cliff in Deepgrove Wyke at NZ 858140.

k. Hawsker Bottoms. The lower boundary of the Grey Shales occurs on the west of Hawsker High Scar at NZ 951077. The dip is at a low angle to the west, and higher beds follow westwards up to the base of the Jet Rock at NZ 948078. The basal beds, the Six Red Nodule beds and beds 28–32 are well exposed, but beds 20–27 are largely obscured and difficult to trace beneath boulders. The top bed of the Ironstone Series, bed 28 (bed 44 of Howarth, 1955 : 154) is rather different at this locality, being a near-continuous bed of red-weathering nodular limestone.

l. Peak, Ravenscar. Immediately east of the Peak Fault at NZ 980027 there is a small exposure of part of the Grey Shales (Howarth 1962 : pl. 27). The top beds of the Ironstone Series and beds 1–11 of the Grey Shales occur near low tide mark, and beds 28–32 occur to the south below the exposure of Jet Rock described previously (Howarth 1962 : 393–395). Beds 12–27 are entirely obscured by boulders. Although it is a small exposure, beds 3 and 5, the lowest three of the Six Red Nodule beds, and the doggers of beds 28 and 30 are well seen, and they do not differ in lithology or thickness from the standard Grey Shales succession on the western side of the Peak Fault. Thus the different lithology found in some higher beds of the Upper Lias on this eastern side of the Peak Fault does not apply to the Grey Shales.


836
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842
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162
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156
155
154
FILLET TAIL DUMP
KETTLENESS
Metres
0
100
200
0
100
500
Feet
Nat. grid prefix: NZ
Base of cliff
Low tide mark
HOLMSGROVE SAND
SUBZONES
Jet Rock
Exaratum
Semicelatum
Tenuicostatum
Clevelandicum
Paltum
Hawskerense
GREY SHALES
Ironstone Series
* Sand, boulders, seaweed

FIG. 3. Geological map of the Grey Shales on the foreshore at Kettleness.

The succession in north-west Cleveland

In marked contrast to the constant Upper Liassic Grey Shales, the Middle Liassic Ironstone Series shows so much lateral variation in thickness and facies that three different successions had to be described for the coastal exposures (Howarth 1955). Later, the development of the Ironstone Series in the Eston area of north-west Cleveland was described by Chowns (1966). Many details of the variable succession were given by Tate & Blake (1876 : 119–152). In that area there is a disconformity at the top of the Main Seam Ironstone, and the overlying " Sulphur Band ", an argillaceous bed full of oolite grains and much pyrites about 0·10 m thick, is correlated with Kettleness bed 26 (Howarth 1955 : 156, = Staithes bed 58). Above the "Sulphur Band" comes the Top Main Dogger, an oolitic ironstone up to 1·00 m thick similar to the Main Seam Ironstone. This is the top of the Ironstone Series and is overlain by the Grey Shales. All the exposures of these beds in the north-west scarp of the Cleveland Hills between Skelton and Osmotherley were visited to examine these horizons. The only place where a satisfactory exposure of the bottom of the Grey Shales could be seen was in a cliff at the side of a stream at Hutton Lowcross (NZ 604134). The Six Red Nodule beds were definitely located, and a thickness of 2·56 m (8 ft 5 in.) of shales was measured below them down to the top of the Top Main Dogger. There is a bed of nodules, possibly Grey Shales bed 5, 0·81 m (2 ft 10 in.) below the top of the shales. It is concluded that the Grey Shales are probably complete down to the bottom of bed 1, and that the Top Main Dogger is the lateral equivalent of Kettleness beds 27 and 28, the top two beds of the Ironstone Series.

This lithological correlation is important because a single specimen of *Dactylioceras pseudocommune* Fucini found in an old ironstone mine at Hob Hill (NZ 653203), near Saltburn, is much the oldest *Dactylioceras* in the English Lias. Its exact horizon was not recorded, but the matrix is a pale green ironstone with white ooliths like both the Main Seam Ironstone and the Top Main Dogger. If it is from the Main Seam its age has to be Apyrenum Subzone, the lower half of the Spinatum Zone, and this would make it the earliest known *Dactylioceras* from anywhere. If from the Top Main Dogger, on the other hand, it would be above the highest *Pleuroceras* and would be taken as indicating the base of the Tenuicostatum Zone. This is compatible with the basal Tenuicostatum Zone age of the earliest *Dactylioceras* in the Mediterranean area, and so it is considered much more likely that the Hob Hill specimen came from the Top Main Dogger than from the Main Seam Ironstone. The lower boundary of the Tenuicostatum Zone is placed, as explained on p. 267, at the base of the Sulphur Band below the Top Main Dogger.

III. PALAEONTOLOGY

Family **DACTYLIOCERATIDAE** Hyatt, 1867

The classification of ammonites of this family poses problems totally different from those of the contemporaneous Hildoceratidae. Ammonites of both families present a bewildering range of morphology until stratigraphical relationships are known. Collections of Hildoceratidae from single horizons show that species are relatively closely defined, and the phenomenon of dimorphism is immediately apparent in many cases. In marked contrast, single bed collections of Dactylioceratidae sometimes present a very large range of continuously variable morphology, and a convincing case of dimorphism has yet to be found. The Dactylioceratidae of the Yorkshire coast Grey Shales have been collected with a degree of stratigraphical control upon which it would hardly be possible to improve. This is because they occur abundantly in nodules or calcified clusters at seven main horizons (i.e. beds 18, 19*b*, 20, 22, 24, 28 and 30), in a sequence that is clearly not condensed, and where each bed of nodules is at a constant horizon (except bed 28). Collections from these beds do not represent single populations in a biological sense, but they do represent single populations in the sense that it is almost certain that no evolution has occurred within the collection from each bed. Each such collection consists of ammonites that exhibit a very large amount of variation in some of the whorl proportions, in rib density, and in the size of the ventro-lateral tubercles. The greatest variation occurs in whorls of between about 50% and 75% of the average adult size: for example in bed 30 whorl height varies between 16 and 23 mm, and umbilical width between 33 and 44 mm, both at 72 mm diameter, while whorl breadth varies very widely between 11 and 24 mm at 50 mm diameter, and the number of ribs per whorl varies between 31 and 85 at the same diameter. Graphs plotted of whorl proportions and rib-density against diameter show that the variation is continuous in each collection, and confirm the impression that there are no morphological breaks in the variation. Whorl breadth and rib-density are interrelated to some extent, for it is specimens with compressed whorls that are more densely ribbed, and those with depressed whorls that are more sparsely ribbed, though the variation in rib-density is still considerable in specimens with similar whorl breadths. There are no specimens with depressed whorls in beds 22 and 24, the variation in whorl breadth being less than one-third of the variation in beds 18, 19, 28 and 30, yet the variation in rib-density in beds 22 and 24 is just as great as at any of the other horizons.

The variation is much less on the final adult whorl, so that all the depressed, tuberculate specimens have more compressed adult body chambers. The specimen figured in Pl. 4, fig. 2 is one of the best examples of highly depressed and strongly tuberculate inner and middle whorls that become completely different on the final adult whorl, which is much more like the specimens with compressed whorls from the same bed. Other such examples are shown on Pl. 1, fig. 3, Pl. 3, fig. 2 and Pl. 9, fig. 1. Specimens showing the full range of morphological variation at each horizon are figured in the plates, and Text-figs. 5 and 6 are graphical representations of the amount of variation.

In erecting a classification for these Grey Shales Dactylioceratidae a choice has to be made between referring all the specimens from one horizon to a single variable species, or dividing up the morphological variation into different species and genera. The amount of variation at each horizon is sufficient to divide the collections into two genera (one compressed, one depressed) and up to four species, according to the scale of differences traditionally adopted by palaeontologists for Dactylioceratidae. The genus *Dactylioceras* (*Orthodactylites*) would be used for the compressed groups, and the name *Kedonoceras* Dagis is available for the depressed groups. The conclusion to be drawn from such a classification is that the three different species of *Kedonoceras* that would be required at different horizons were more closely related to each other than they were to the species of *Dactylioceras* (*Orthodactylites*) that each of them accompanied. Yet the variation at each horizon appears to be continuous between the end forms, so the splitting into species and genera would be by means of arbitrary morphological divisions ; moreover, the adult body chambers of all the species of " *Kedonoceras* " revert to a morphology much closer to the accompanying compressed species, so that the term *Kedonoceras* would really have only been applied to the inner and middle whorls.

These considerations have led to the belief that it is better, and probably phylogenetically more correct, to refer all the specimens at each horizon to a single variable species of *Dactylioceras* (*Orthodactylites*). The form of the adults and the continuity of the variation seem to indicate that the depressed forms are more closely related to the compressed forms at the same horizon than they are to the depressed forms at other horizons. Examination and analysis of the whole collection has led to the recognition of four successive species : one in bed 18, one in bed 19*b*, one in beds 20, 22, 24 and 26 which shows minor sub-specific evolutionary trends, and finally one in beds 28 and 30–32. These four species are largely distinct from one another in all their forms, and only in the case of the highest and the lowest species are some of the forms sufficiently alike to make separation difficult. Three of the four subzones erected in this paper are based on the stratigraphical succession of these four species. Division of the collection in a different way according to traditional morphology would not make any difference to the stratigraphical results.

Taxonomy according to these methods and stratigraphical control leads to an entirely different classification from that obtained by means of orthodox morphological taxonomy. Thus, in a recent work, Pinna & Levi-Setti (1971) erected a morphological classification for Mediterranean Dactylioceratidae that had little accurate stratigraphical control. The oversplitting that resulted and the separation of closely similar forms (e.g. *Nodicoeloceras* and *Mesodactylites*) would probably break down if stratigraphical associations were known. One such association which is accurately known is that of *Porpoceras* in Yorkshire : the fauna occurs only in beds xlii and xliii of the Braunianus Subzone at Ravenscar (Howarth 1962 : 400), and specimens show a wide range of variation in whorl breadth that is the basis of the three specific names *P. vortex* (Simpson), *P. verticosum* Buckman and *P. vorticellum* (Simpson). The variation is continuous and the whole fauna is linked together by features of the ribbing that are characteristic of *Porpoceras*. According to the taxonomy adopted here the whole fauna would be referred to the single species *P. vortex* ; even if the three species were upheld, they would have to be referred to *Porpoceras* ; but Pinna & Levi-Setti (1971 : 107, 121) placed *P. verticosum* and *P. vorticellum* in *Nodicoeloceras* (a genus said to belong to the Mediterranean subfamily " Mesodactylioceratinae ") and *P. vortex* in *Peronoceras* (a genus of the north-west European " Dactylioceratinae "). Faunal associations like *Porpoceras* are the basic units on which a classification should be built, and any classification which splits them up into different genera said to belong to different provinces must fail.

The north-east Siberian genus *Kedonoceras* Dagis (1968) probably consists of the depressed variants of Tenuicostatum Zone *Dactylioceras* (*Orthodactylites*), some of them possibly conspecific with those in the Yorkshire Grey Shales. As in Yorkshire they occur below faunas of *Tiltoniceras*. All the known specimens are small (up to 53 mm diameter), and in the absence of any adults it is not possible to be certain where they belong. The subfamily name Kedonoceratinae proposed for them, and to include also the totally unrelated Bifrons and Variabilis Zone genera *Porpoceras*, *Collina* and *Catacoeloceras*, cannot be accepted as a grouping for these mainly depressed forms, that have a suture-line shape dependent of the shape of the whorl. The depressed forms known as *Kedonoceras* are more closely related to the *Dactylioceras* (*Orthodactylites*) that they accompany than they are to any other depressed Dactylioceratidae. The placing of *Kedonoceras* in the synonymy of *Porpoceras* by Guex (1971 : 231) is another example of how a classification based mainly on morphology can bring together two forms that are widely separated stratigraphically and not related in any way.

The Grey Shales Dactylioceratidae show no evidence of dimorphism. A considerable number of adult specimens are known (more than 100 were examined) and in each species the size range of adults forms a single group with an even distribution between largest and smallest. The ratio of largest to smallest adults in the four species recognized is 1·55, 1·67, 1·46 and 1·60. These figures are considerably less than the ratios of 2·0 to 3·0 that have been found for each dimorph of several dimorphic species of Hildoceratidae. There is no other evidence for dimorphism in the Grey Shales species. Dimorphism in Dactylioceratidae was first claimed by Lehmann (1968) for two species : in *D. ernsti* one dimorph was said to be 55–60 mm diameter, the other 90 mm, there being no other differences, a distinction that is not considered here to be sufficient to claim dimorphism ; in *D. athleticum* one dimorph was said to be 40–47 mm diameter, the other 67–93 mm, and there are apparently consistent differences in the spacing of the first 12 septae. Again the evidence is not thought sufficient to uphold it as a case of dimorphism. The recognition of dimorphism throughout the Dactylioceratidae has been claimed by Guex (1971), but the number of known specimens that could be microconchs is very small. Most of them could be abnormal or could be specifically different from the macroconchs that they are said to accompany. The evidence for dimorphism is summed up in the Yorkshire occurrences : Hildoceratidae and Dactylioceratidae existed together during much of the Upper Lias ; the Hildoceratidae show abundant evidence of dimorphism, the Dactylioceratidae show none.

Shell structure and preservation

The appearance of the Grey Shales Dactylioceratidae is greatly influenced by the unique shell structure of ammonites of that family. Many cases are known of the deposition of various shell structures within the body chambers of ammonites, such as the floor cutting off an originally hollow keel, septae at the base of long spines or tubercles, and a dorsal shell (or callus) laid down on top of the ventral part of the shell of the previous whorl to fill in irregularities of the ornament. But a continuous inner shell lining the whole of the lateral and ventral parts of the inside of the main shell has only been found so far in Dactylioceratidae, and was first described by Guex (1970). The point of formation of this inner shell is between one-eighth and one-quarter of a whorl behind the mouth border, and the front growing edge is angled forwards from the umbilical seam to the venter at about 45° to the radial line. The inner shell fills in the ornament of the main shell to a great extent, cutting off cavities inside the ribs which have characteristic flat floors, and the relief of the ribs on the inside of the inner shell is only a small fraction of the relief of the ribs of the main shell. The inner shell is continuous over the ventral and lateral parts of the main shell up to the umbilical seams, and is apparently absent or only partly formed on the dorsum between the umbilical seams. The absence of the inner shell on the dorsum is clearly seen on some very well-preserved Dactylioceratidae from west Northamptonshire, but one of the Grey Shales specimens (Text-fig. 4B) shows what is apparently dorsal infilling of some of the spaces between the ribs on the venter of the previous whorl, by means of layers of shell near the top of the intercostal spaces which cut off cavities below (CD on Text-fig. 4B). The position of commencement of the inner shell on the inner whorls is uncertain. The characteristic flat-topped ribs start 2½ to 2¾ whorls before the adult mouth border in the Grey Shales specimens, and there is evidence that the inner shell occurs on at least one further inner whorl, but without forming cavities in the ribs of the main shell. So the inner shell starts on the 4th whorl before the adult aperture or earlier (complete specimens of *Dactylioceras* have approximately 7 whorls).

Polished sections of parts of several Grey Shales specimens were prepared to show the shell structure, and drawings made from two of them are shown in Text-fig. 4. Both are from near the middle of the venter ; fig. 4A is from an adult body chamber, while fig. 4B is from a phragmocone rather more than one whorl before the mouth border, and shows parts of the siphuncle and the septa, which were laid down after the inner shell. The shell structure on the lateral parts of the whorl is similar, and in specimens with ventro-lateral spines the inner shell forms an arched floor at the base of each spine. In all the Grey Shales specimens the cavities in the ribs between the main and inner shells are filled with secondary calcite or occasionally with iron pyrites, but the cavities in well-preserved Northamptonshire Dactylioceratidae are empty.

The main shell consists of the three layers that are normally found in ammonites : a thin Outer Prismatic Layer, a thick Nacreous Layer and a thin Inner Prismatic Layer. So far as can be ascertained the inner shell consists of a fairly thick outer nacreous layer and a thin inner layer of prismatic crystals.

Grey Shales Dactylioceratidae have four basically different surface appearances according to the shell layer surface that is seen :

(1) The outer surface of the main shell is rarely seen, because most specimens are preserved inside nodules and there is strong adhesion between the main shell and the enclosing matrix. Occasionally this surface is seen on the last part of the body chamber near the mouth border when the main shell remains attached to the ammonite, but in most cases the shell breaks off with the enclosing matrix. When

seen, this shell surface has broadly rounded ribs with deep intercostal spaces of similar width to the ribs. Examples of this preservation are seen in Pl. 1, fig. 1, the final $\frac{1}{3}$ whorl of Pl. 1, fig. 4, Pl. 2, fig. 4, Pl. 8, fig. 4 and Pl. 9, fig. 3. Sometimes the main shell is preserved intact on the inner whorls, while missing on the outer two whorls. Thus on the inner whorls of Pl. 4, fig. 2 most of the main shell is preserved, with one or two of the spines nearly complete.

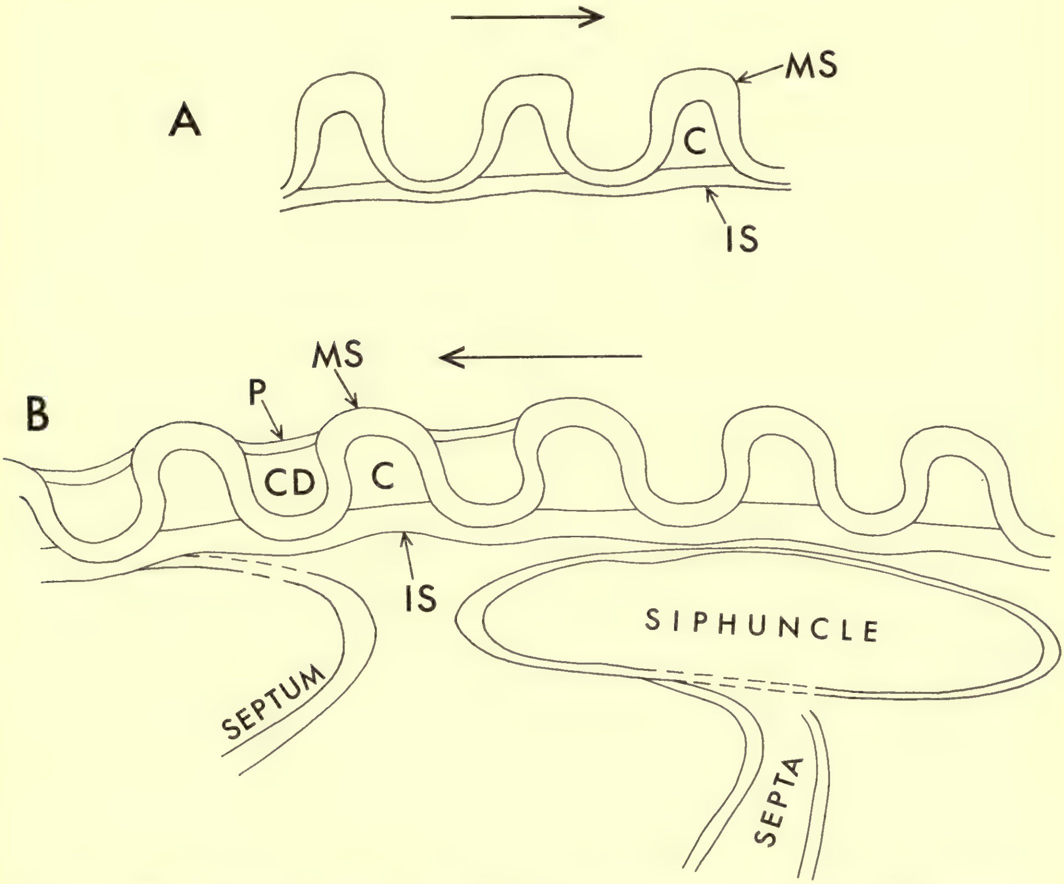

FIG. 4. Shell structure in two specimens of *Dactylioceras semicelatum* (Young & Bird). Sections through the shell showing: MS—the main (outer) shell. IS—the inner shell. C—the cavity between main and inner shells, now filled with secondary calcite or iron pyrites. P—partitions cutting off some of the intercostal spaces, laid down as dorsal shell of the next outer whorl. CD—the cavity between the main shell and the dorsal partitions of the next outer whorl, now filled with secondary calcite. Arrows indicate direction of the aperture. A—section near the middle of the venter of the adult body chamber, one-third of a whorl before the mouth border. C.77306, bed 30, east Kettleness. × 11. B—section at the middle of the venter of the phragmocone 1 $\frac{1}{16}$ whorls before the adult mouth border. An oblique section through the siphuncle and parts of three septa are seen. C.77317 (Pl. 9, fig. 1), bed 30, Hawsker Bottoms. × 11.

(2) An internal mould of the inner surface of the main shell is seen near the apertures of most specimens that are complete to the mouth border, and when the shell breaks off with the enclosing matrix. The ribs are of high relief, but are noticeably thinner than in (1) above, and the intercostal spaces are much wider. Many of the complete adults figured in the plates show this type of preservation on the final part of the outer whorl: e.g. Pl. 2, fig. 2, Pl. 3, figs. 1, 2, Pl. 5, fig. 2 and Pl. 6, fig. 3, in all of which the ribs are of much higher relief on the final part of the whorl due to the absence of the inner shell.

A different occurrence of the preservation of the form of the inner surface of the main shell occurs when the inner shell is attached to the ammonite and calcite casts of the cavities between the two shells (C in Text-fig. 4) remain in place. The whole forms a perfect replica of the inside surface of the main shell, but is only occasionally found.

(3) The commonest type of preservation in the Grey Shales Dactylioceratidae is with the inner shell attached to the ammonite after the main shell has broken away with the enclosing matrix. The outer surface of the inner shell has characteristically flat-topped ribs of relatively low relief, and this is the type of ornament seen in most of the specimens that have shell attached which are figured in the plates. Good examples are Pl. 6, fig. 2, Pl. 7, figs. 1 and 2, and Pl. 8, figs. 1 and 2, in all of which the flat-topped ribs can be seen. In some specimens of *Dactylioceras semicelatum* from beds 28 and 30 the inner shell is replaced by iron pyrites in the phragmocone, so that a cast in pyrites of the outer surface of the inner shell is seen. This usually occurs in patches, and there are areas where the pyritic replacement merges into original shell. The specimen in Pl. 8, fig. 2 is preserved in this way, and approximately half the figured side is a pyritic cast of the inner shell. The whole of the phragmocone of Pl. 7, fig. 1 is similarly preserved, but in this case many intercostal parts of unaltered (i.e. calcitic) main shell remain attached to the pyrites-replaced inner shell. In a few places pyritic casts of the cavities between the main and inner shells are preserved. This pyrites-replaced inner shell overlies recrystallized calcite inside the phragmocone, and in a zone of partial replacement near the final septum the outer surface of the inner shell has a skin of pyrites. On the body chamber the inner shell is calcitic and overlies an internal mould of pyrites.

(4) When both the main and inner shells break off, the ammonite consists of an internal mould showing the ornament of the inner surface of the inner shell. The ribs and intercostal spaces are smoothly rounded and of much lower relief than either surface of the main shell. Most parts of the specimens figured in Pl. 1, fig. 2, Pl. 2, fig. 2, Pl. 3, figs. 1 and 2, Pl. 4, fig. 2 (outer whorl), Pl. 5, fig. 2 and Pl. 6, fig. 3 are preserved in this way.

Genus ***DACTYLIOCERAS*** Hyatt, 1867

TYPE SPECIES: *Ammonites communis* J. Sowerby, 1815, designated ICZN Opinion 576, 1959.

The general characters and long synonymy of *Dactylioceras* can be found in the *Treatise on Invertebrate Paleontology*, vol. L, p. 252. They are not discussed here, for this description is concerned with only a single specimen of one of the earliest known species of *D.* (*Dactylioceras*), and with abundant faunas of the subgenus *Orthodactylites.*

Dactylioceras (Dactylioceras) pseudocommune Fucini

Pl. 1, fig. 1

1876 *Stephanoceras holandrei* (d'Orbigny) ; Tate & Blake : 172, 299–300.
1935 *Dactylioceras pseudocommune* Fucini : 86, pl. 9, figs. 1–3.
1935 *Dactylioceras pseudocrassulosum* Fucini : 87, pl. 9, figs. 6–8.
1935 *Dactylioceras peloritanum* Fucini : 88, pl. 9, figs. 14, 15.
1935 *Dactylioceras subholandrei* Fucini : 89, pl. 9, fig. 17.
1935 *Dactylioceras inaequicostatum* Fucini : 89, pl. 9, fig. 16.
? 1966 *Dactylioceras mirabile* Fucini ; Fischer : 24, pl. 1, fig. 6 ; pl. 4, fig. 1.
1966 *Dactylioceras pseudocommune* Fucini ; Fischer : 26, pl. 1, fig. 5 ; pl. 4, figs. 3, ? 6.
1971 *Dactylioceras* (*Dactylioceras*) *pseudocommune* Fucini ; Pinna & Levi-Setti : 37, pl. 1, fig. 8.

MATERIAL. One specimen, Institute of Geological Sciences, London, GSM 22568, from the old ironstone mine at Hob Hill (NZ 653203), near Saltburn. Paltum Subzone, lower part. R. Tate collection.

DESCRIPTION. As discussed elsewhere (p. 246) this specimen almost certainly came from the Top Main Dogger and, from low in the Paltum Subzone only just above the base of the Upper Lias, is the oldest well-preserved *Dactylioceras* known in Britain.

It consists of one-third of a whorl of approximately 65 mm diameter ending in a broken aperture, and parts of the next two inner whorls are attached. The whorls are evolute, and the whorl section has flat sides and a broadly arched venter. Near the aperture the whorl height is 16·3 mm, and the whorl breadth is 14·5 mm. The ribs are high, sharp and straight ; most bifurcate at a small ventro-lateral tubercle, and the ribs then curve forwards and are continuous across the venter. Occasional ribs remain single : there are 14 bifurcating and 2 single ribs on the outer whorl of the fragment, giving a total of 30 secondary ribs on the venter. The umbilical seam just touches the ventro-lateral tubercles on the next inner whorl, and the secondaries are concealed. No traces of septae or suture-lines are to be seen on any of the whorls.

Reference is made to *Dactylioceras* s.s. because of the predominance of bifurcating ribs and ventro-lateral tubercles, and lack of the annular ribbing of *Orthodactylites.* The earliest group of species of *Dactylioceras* is best known from Taormina, Sicily, from the descriptions of Fucini (1935), and there is now good evidence from that area and other parts of Italy (see p. 271) that the group marks the base of the Tenuicostatum Zone. Specimens are common and it is probable that 2 species of *Dactylioceras* s.s. and 2 of *D.* (*Orthodactylites*) are present (Pinna & Levi-Setti 1971 : 90). The Hob Hill ammonite compares closely with the lectotype of *D. pseudocommune* Fucini (1935 : pl. 9, fig. 1). Nine other specimens figured by Fucini (see synonymy above) are considered to be conspecific, for all have low-density, straight ribs bifurcating at ventro-lateral tubercles. Other species from the same fauna are *D.* (*D.*) *simplex* Fucini (1935 : 86, pl. 9, figs. 4, 5) which has trifurcating ribs, and therefore many more secondaries, and *D.* (*Orthodactylites*) *mirabile* and *polymorphum* Fucini, both with bifurcating and single ribs. *D.* (*D.*) *pseudocommune* also occurs in northern Italy (Pinna & Levi-Setti 1971 : 89, pl. 1, fig. 8), apparently low in the Tenuicostatum Zone, and the single figured specimen closely resembles the Hob Hill ammonite. Ammonites belonging to the same group of species occur at Kammerker, Austria, but in Fischer's (1966) description the Tenuicostatum Zone is dealt with as a single unit and the divisions into species are not based on stratigraphical associations. Some specimens (e.g. Fischer 1966 : pl. 4, figs. 1, 3, 6) do appear to be *D.* (*D.*) *pseudocommune*. Other possible occurrences in Algeria and Portugal are not supported by figured specimens. The group is mainly Mediterranean in distribution, and the Hob Hill specimen is the first record in north-west Europe. Its age in Yorkshire, at the base of the Paltum Subzone of the Tenuicostatum Zone, is good confirmation of the basal Tenuicostatum Zone age of this earliest group of species of *Dactylioceras* in Italy.

Dactylioceras sp. indet.

The existence of *Dactylioceras* in other parts of the Paltum Subzone is indicated by two specimens that are included here for record purposes.

1. A 36 mm diameter crushed *Dactylioceras* s.l. was found on the upper surface of bed 3 on the east side of Kettleness. Although poorly preserved, fairly widely spaced primary ribs and approximately twice as many secondary ribs can be seen, and it may belong to the earliest known group of species of *Dactylioceras* discussed above.
2. The impression of a venter of a *Dactylioceras* s.l. preserved solid, presumably in a nodule, was seen at about the middle of bed 6 in the bank of a stream at Hutton Lowcross (NZ 604134). The impression did not extend as far as the ventro-lateral angle.

Subgenus ***ORTHODACTYLITES*** Buckman, 1926

TYPE SPECIES : *O. directum* Buckman, 1926, by original designation.

SYNONYMS : *Kryptodactylites* Buckman, 1926 (type species : *Ammonites semicelatus* Simpson, 1843, by original designation) ; *Tenuidactylites* Buckman, 1926 (type species : *Ammonites tenuicostatus* Young & Bird, 1822, by original designation).

DIAGNOSIS. *Dactylioceras* with annular, rectiradiate or prorsiradiate ribs. Rib-density moderate to high, occasionally distantly ribbed on some whorls. Single ribs as well as bifurcating ribs occur commonly at some growth stage. Whorl shape varies from compressed to highly depressed. Ventro-lateral tubercles or spines may occur on forms with depressed whorls, and ribs may be looped to them in fibulate style.

DESCRIPTION. *Orthodactylites* is a subgeneric name for a group of species, occurring mainly in the Tenuicostatum Zone, that have annular ribs, some of which are single (i.e. not bifurcating) at least at some growth stage. Five species are found in British rocks. The type species *O. directum* Buckman (synonym : *O. mitis*

Buckman, 1927) occurs in the Transition Bed and the Marlstone Rock Bed from Lincolnshire to Gloucestershire, and is the only English species that does not occur in Yorkshire. The four Yorkshire species are *D.* (*O.*) *crosbeyi* (Simpson, 1843), *D.* (*O.*) *clevelandicum* sp. nov., *D.* (*O.*) *tenuicostatum* (Young & Bird, 1822) and *D.* (*O.*) *semicelatum* (Simpson, 1843). They are confined to the Tenuicostatum Zone and the type specimens of all four come from the Yorkshire Grey Shales. The last two species also occur in other parts of England, but the description below is concerned only with the Yorkshire occurrences. The earliest species of *Orthodactylites* are *D.* (*O.*) *mirabile* and *polymorphum* Fucini, originally described from Sicily (Fucini 1935), and also known from northern Italy, Austria and probably Algeria and Portugal (Pinna & Levi-Setti 1971 : 37). In northern Italy and Austria their age is known to be Tenuicostatum Zone, but in Sicily their age is not accurately determinable and they may also occur in the top of the Spinatum Zone. The last species of *Orthodactylites* (as yet undescribed) occurs in the Exaratum Subzone in England.

Dactylioceras (Orthodactylites) crosbeyi (Simpson)

Pl. 1, figs. 2–4; Pl. 2, figs. 1–4

1843 *Ammonites crosbeyi* Simpson : 22.
1855 *Ammonites crosbeyi* Simpson : 58.
1884 *Ammonites crosbeyi* Simpson : 90.
1912 *Coeloceras crosbeyi* (Simpson) ; Buckman : pl. 60.
? 1957 *Dactylioceras pseudosemicelatum* Maubeuge : 193, pl. 3, fig. 6.
? 1957 *Dactylioceras podagrosum* Maubeuge : 193, pl. 4, fig. 7.

TYPE. The holotype is Whitby Museum no. 134, and was figured by Buckman (1912 : pl. 60). It comes from bed 18 of the Grey Shales, from a locality not known more accurately than " Whitby ". Dimensions (in the order : whorl height, whorl breadth, umbilical width) : at 74 mm diameter : 23·5 (0·32), —, 32·5 (0·44) ; at 48 mm diameter, whorl breadth is 24·7 mm (0·51) ; 69 ribs at 76 mm diameter.

DISTRIBUTION. Clevelandicum Subzone. Occurs only in Grey Shales bed 18, from which 69 specimens were collected (list on p. 241).

DIAGNOSIS. Whorls one-third to one-quarter involute, large whorl height, moderately wide umbilicus. Whorl section varies from sub-circular with approximately equal height and breadth, to highly depressed, where breadth/height ratio is up to 2·3 at diameters of 50 to 70 mm. Venter of depressed forms very wide and arched, and small ventro-lateral tubercles formed. Body chamber always becomes more compressed. Adult size 84 to 130 mm diameter, length of adult body chamber 15/16 to 17/16ths of a whorl. Ribs straight, slightly prorsiradiate, bifurcating or single, very variable in density.

DESCRIPTION. This species occurs only in bed 18, preserved in small calcareous nodules, or calcified masses of a few ammonites lying at all angles, at a single horizon at the middle of that bed. The preservation is only moderate, for in most cases the body chamber is preserved solid on one side and partly crushed on the other, while the inner whorls are crushed, distorted or missing. Only rarely are the inner whorls preserved solid, and few specimens are sufficiently well preserved for measurements of whorl proportions and rib counts to be made.

D. (*O.*) *crosbeyi* is characterized by fairly high and thick whorls, about one-third to one-quarter involute (so that the umbilicus is moderately wide), and by fine to moderate rib-density. Some specimens, especially those with depressed whorls, have small ventro-lateral tubercles on all whorls except the final one, but others have no tubercles. Nine of the specimens collected have complete, adult body chambers, and the diameter at the final mouth border varies between 84 and 130 mm (average 101 mm). The length of the complete body chamber in six specimens varies between 15/16 and 17/16ths of a whorl. In all of them the final whorl has height and breadth about equal, or is slightly more compressed, and the ribs are moderate to dense (80–90 on the final whorl) with single and bifurcating ribs usually alternating, but more ribs become single near the end of the body chamber. Two examples with body chambers are figured in Pl. 1, fig. 2 and Pl. 2, fig. 2; some have inner whorls similarly compressed and fine-ribbed (e.g. Pl. 1, fig. 4), but others show great variation, and there is apparently complete gradation to highly depressed coronate inner whorls, in which the whorl breadth is probably greater than in any other Dactylioceratid ammonites. Three coronate inner whorls are figured in Pl. 2, figs. 1, 3 and 4; in the largest, at a diameter of about 70 mm, the whorl height is 18·5 mm, the breadth about 42 mm, giving a whorl breadth/height ratio of 2·3. The other two have ratios of 2·25 and 2·1 at smaller diameters. These inner whorls have small ventro-lateral tubercles or spines. The body chambers of such specimens become more compressed and the tubercles are lost (Pl. 1, fig. 3), and they are similar to the body chambers of specimens with compressed inner whorls. A collection with this large amount of variation is referred to only one species because they all come from a single horizon of nodules in a succession that is not condensed, there is complete gradation in variation between the markedly different end forms, and the adult body chambers are similar with a much smaller amount of variation.

D. (*O.*) *crosbeyi* has higher and thicker whorls and is more involute than *D.* (*O.*) *clevelandicum* or *tenuicostatum*. It has fewer ribs than the latter species, but is largely similar in rib-density to the former species. Differences from *D.* (*O.*) *semicelatum* are less marked, but the whorl height in *crosbeyi* is somewhat higher, overlapping only the upper half of the variation in *D.* (*O.*) *semicelatum*, and the holotype of *crosbeyi* has higher whorls than any *semicelatum*. Correspondingly the umbilical width is generally smaller in *crosbeyi* and the amount of involution more. The thick-whorled examples of *D. crosbeyi* are much thicker than any other species, and the holotype lies on the higher border of the range of variation in *clevelandicum* and *semicelatum* (see Text-fig. 5).

The only possible record of *D.* (*O.*) *crosbeyi* outside Yorkshire is the two specimens figured by Maubeuge (1957 : 193, pl. 3, fig. 6; pl. 4, fig. 7) as the holotypes of *D. pseudosemicelatum* and *D. podagrosum* from eastern France. Without larger specimens from the same bed these two are difficult to determine, but they do appear to have thick whorls and non-tuberculate ribs like some specimens of *D. crosbeyi*, so it is possible that they are synonyms of that species.

Interpretation of *Ammonites annulatus* J. Sowerby, 1819

It has been stated previously by Sylvester-Bradley (1958 : 67) and Howarth (1962 : 410) that *D. crosbeyi* is a synonym of *Ammonites annulatus* J. Sowerby (1819 : 41, pl. 222, fig. 5 only), when the latter species is restricted to its lectotype as selected by Oppel (1856 : 255). This is not correct, for that lectotype is a fine specimen of *Nodicoeloceras crassoides* (Simpson, 1855) from bed 18/19, Falciferum Subzone, of the Ilminster–Barrington/Stocklinch succession. Its matrix agrees with that of other ammonites collected from that bed, and it is considerably different in matrix and morphology from specimens of *Dactylioceras* (*Orthodactylites*) that come from the thin representative (beds 1 and 2) of the Tenuicostatum Zone in that area. It is a large specimen with a complete adult body chamber 1¼ whorls long, on which the bifurcating ribs of earlier whorls give way to an alternation of bifurcating and single ribs. In this respect the last whorl resembles *Orthodactylites*, but it differs from *D.* (*O.*) *crosbeyi* in having thick inner whorls with a rounded cross-section and no tubercles. Sowerby's specific name *annulatus* cannot be used instead of *crassoides*, because it is a junior homonym of *Ammonites annulatus* Schlotheim, 1813.

Dactylioceras (Orthodactylites) clevelandicum sp. nov.

Pl. 3, figs. 1–3 ; Pl. 4, figs. 1, 2 ; Pl. 5, fig. 3

TYPE. The holotype is C.77017 (Pl. 3, fig. 1) from bed 19*b* at Holmsgrove Sand. It is a complete specimen with 13/16ths of a whorl of body chamber ending in a contracted mouth border at 79 mm diameter, and has the following dimensions : at 77 mm diameter : 17·0 (0·22), 17·2 (0·22), 44·5 (0·58) ; 85 ribs at 78 mm diameter, 71 at 66 mm, 65 at 58 mm, 52 at 30 mm, 46 at 21 mm.

DISTRIBUTION. Clevelandicum Subzone. Grey Shales bed 19*b*, from which 199 specimens were collected.

DIAGNOSIS. Whorls evolute, small whorl height, wide umbilicus. Whorl section varies from rounded with equal height and breadth, to depressed with breadth/height ratio of up to 1·7 at 50 to 70 mm diameter. Ribs straight, rectiradiate, single and bifurcating, highly variable moderate to low rib-density. Ventrolateral tubercles or spines and fibulate ribbing occurs on some depressed whorls. Adult body chamber with many single ribs, no tubercles, more compressed than depressed inner whorls. Adult size 67 to 112 mm diameter, length of body chamber 13/16 to 16/16ths of a whorl.

DESCRIPTION. This species occurs in large numbers in calcified masses at the same horizon as the thin red-weathering nodules of bed 19*b*. All the exposures of that bed yielded some specimens, but particularly good localities from which large collections were made are the east side of Kettleness and Holmsgrove Sand. Several specimens are usually clustered together, all in different orientations, and calcification is confined to the immediate vicinity of the ammonites so that substantial nodules are not formed. Preservation is usually very good, with inner whorls and most of the body chamber solid and intact in many specimens. Such good material has enabled whorl dimensions to be measured in 40 specimens and rib counts on 55 specimens.

D. (*O.*) *clevelandicum* is very evolute, with little overlap of the whorls, and so has a consistently small whorl height and wide umbilicus (Text-fig. 5). However, it shows a large amount of variation in whorl breadth and in rib-density (Text-fig. 6). The holotype has compressed whorls and a moderate to high rib-density. Other specimens, similarly compressed, have fewer ribs (Pl. 4, fig. 1), and there is then a complete series of gradations involving increasing whorl breadth and appearance of tubercles (Pl. 5, fig. 3; Pl. 3, fig. 3), ending with highly depressed tuberculate inner whorls (Pl. 3, fig. 2; Pl. 4, fig. 2). In the latter type the adult body chamber reverts to a non-tuberculate more compressed form, and the whorl thickness near the end of the body-chamber may be less than that of the previous whorl. In highly depressed specimens the ventro-lateral tubercles are spinose and fibulate. This large amount of variation in whorl thickness and rib-density is shown in Text-figs. 5 and 6; measurements from specimens are scattered evenly over the graphs from which these diagrams were drawn showing that the variation is continuous, though there are more moderate to finely ribbed specimens (like the holotype), than depressed, tuberculate specimens. The adult body chamber ends in a slightly contracted mouth border, and in 17 adults the diameter at the mouth border varies between 67 and 112 mm (average 85 mm). The length of these body chambers varies between 13/16 and 16/16ths of a whorl.

D. (*O.*) *clevelandicum* differs from *crosbeyi* and *semicelatum* in having slender more evolute whorls, and larger spinose tubercles on those with depressed inner whorls. It does not differ from either species in rib-density. *D.* (*O.*) *tenuicostatum* has slender evolute whorls, is always compressed and is more densely ribbed than *clevelandicum*; there is little overlap in the rib-density variation of the two species. *D.* (*O.*) *clevelandicum* is not known from outside Yorkshire.

Dactylioceras (Orthodactylites) tenuicostatum (Young & Bird)

Pl. 5, figs. 1, 2; Pl. 6, figs. 2, 3

1819 *Ammonites annulatus* J. Sowerby: 41, pl. 222, fig. 1 only (*non* Schlotheim, 1813).
1822 *Ammonites tenuicostatus* Young & Bird: 247, pl. 12, fig. 8.
1828 *Ammonites annulatus* Sowerby; Young & Bird: 253, pl. 12, fig. 11.
1884 *Stephanoceras annulatum* (J. Sowerby); Wright: 475, pl. 84, figs. 7, 8.
1920 *Dactylioceras tenuicostatum* (Young & Bird) Buckman: pl. 157.
1927 *Tenuidactylites tenuicostatus* (Young & Bird) Buckman: pl. 157A.
1933 *Dactylioceras tenuicostatum* (Young & Bird); Arkell: pl. 32, fig. 6.
1956 *Dactylioceras tenuicostatum* (Young & Bird); Arkell: pl. 33, fig. 6.
1957 *Dactylioceras tenuicostatum* (Young & Bird); Maubeuge: 208, figs. ? 41, 42, 43.
1961 *Dactylioceras tenuicostatum* (Young & Bird); Dean, Donovan & Howarth: pl. 72, fig. 1.

TYPE. The holotype is known to be lost (Howarth 1962*a*: 116). The neotype, here designated, is C.77182 (Pl. 5, fig. 1) from bed 22 exposed immediately east of Port Mulgrave harbour. It is a complete adult with a body chamber 14/16ths of a whorl long, ending in a contracted aperture at 89 mm diameter. Its dimensions

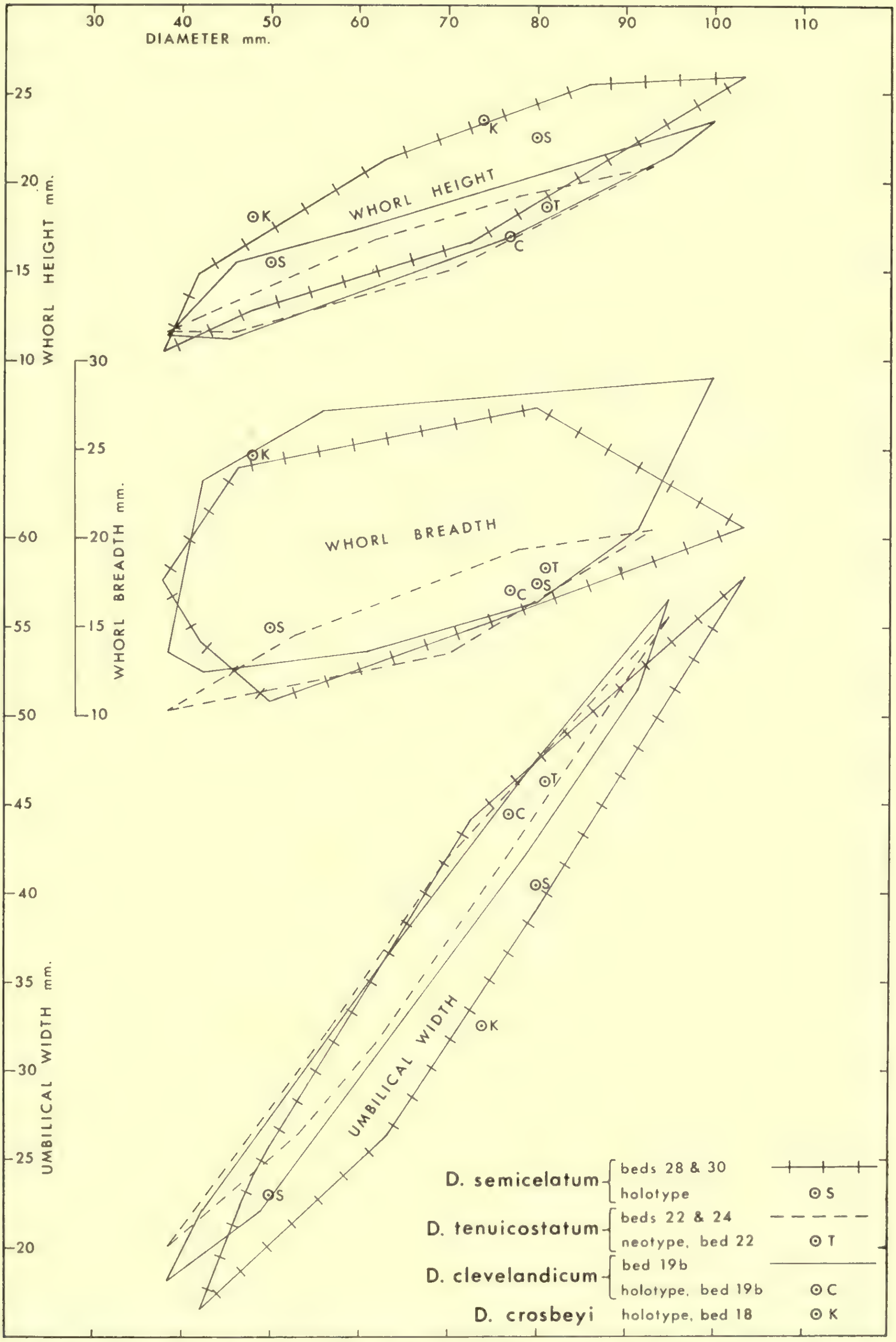

Fig. 5. Envelopes of scatter diagrams of whorl dimensions of Grey Shales species of *Dactylioceras* (*Orthodactylites*), plotted from measurements from 34 specimens of *D.* (*O.*) *semicelatum*, 31 of *D.* (*O.*) *tenuicostatum* and 41 of *D.* (*O.*) *clevelandicum*.

are : at 81 mm diameter : 18·7 (0·23), 18·4 (0·23), 46·4 (0·57) ; 123 ribs at 85 mm diameter, 108 at 75 mm, 100 at 65 mm, 81 at 48 mm, 64 at 30 mm.

Distribution. Tenuicostatum Subzone. Grey Shales beds 20–26, from which 179 specimens were collected.

Diagnosis. Whorls evolute, small whorl height, wide umbilicus, whorl breadth always slightly less than or equal to whorl height. No depressed forms. Ribs straight, fine, approximately rectiradiate, but prorsiradiate on inner whorls, single or bifurcating, high but variable rib-density. No tubercles. Adult size 72 to 105 mm diameter, length of body chamber 13/16 to 18/16ths of a whorl.

Description. The holotype was Whitby Museum no. 81, which is now lost, and there is no evidence for the existence of any other specimens in the type series. Identifications of this widely quoted species have been based on the well-preserved Whitby topotypes figured by Wright (1884 : pl. 84, figs. 7, 8), Buckman (1920 : pl. 157 ; 1927 : pl. 157A) and Dean, Donovan & Howarth (1961 : pl. 72, fig. 1). There is no doubt that these four topotypes came from beds 22 or 24 of the Yorkshire coast Grey Shales, and one of them, the specimen figured by Buckman (1920 : pl. 157), was said to be the neotype by Dean, Donovan & Howarth (1961 : 476). This neotype designation was defective in several ways : it did not fulfil the conditions of Art. 75 (c) (1), (5) and (6) of the Code of Zoological Nomenclature, because the characters differentiating the species were not given, the specimen was insufficiently documented, and it is now thought to be lost. The position can be retrieved by formally designating C.77182 as neotype, a specimen collected by myself just east of Port Mulgrave harbour. The exact horizon and locality of Young & Bird's holotype is not known, but it must have come from bed 22 or 24 of the Yorkshire coast Grey Shales, so C.77182 is a suitable specimen to be a neotype, especially as it is a well-preserved complete adult showing average characters for the species.

Almost all the small spherical nodules of beds 22 and 24 at all the localities contain a single specimen of *D.* (*O.*) *tenuicostatum* lying horizontally through the centre. Rarely nodules contain two or more smaller specimens. The nodule is generally larger than the ammonite it contains, and preservation is excellent, with all whorls up to the final mouth border intact. The inner whorls of some specimens are partly pyritized.

D. (*O.*) *tenuicostatum* has slender, evolute whorls with a small whorl height and a wide umbilicus. The whorl breadth is equal to or slightly less than the whorl height, and there are no examples with depressed whorls. In this respect it shows much less variation than any of the other species described here (Text-fig. 5), all of which have variants with depressed whorls. In rib-density, however, *tenuicostatum* has as much variation as the other species (Text-fig. 6). Sufficient measurements were made for the faunas from beds 22 and 24 to be plotted separately, and it can be seen from Text-fig. 6 that specimens in bed 24 have a slightly higher average rib-density than those in bed 22, although there is a very large percentage overlap between the two. The amount of variation in rib-density in *tenuicostatum* is just as large as in *clevelandicum*. There are no tubercles in *tenuicostatum*. The

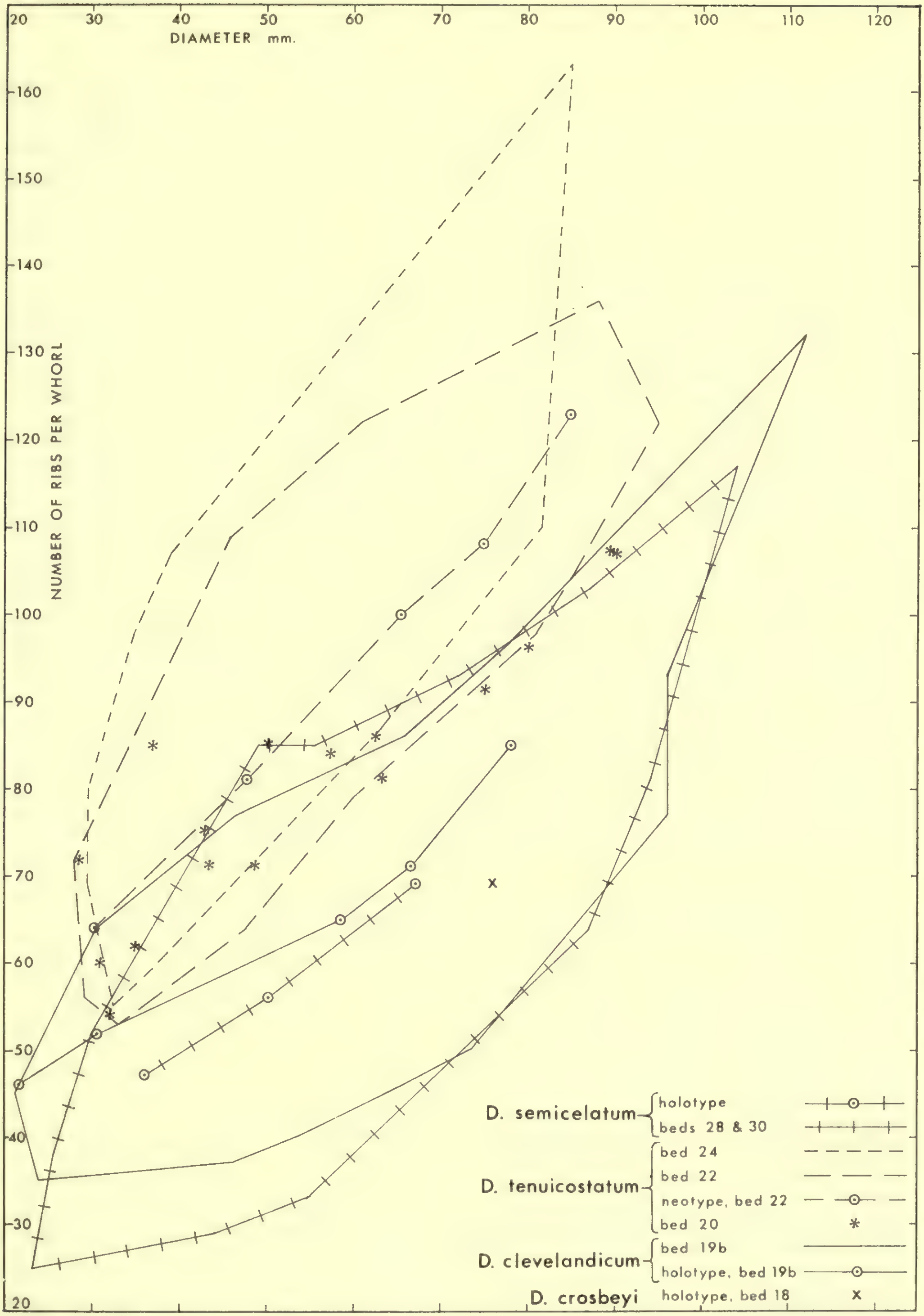

FIG. 6. Envelopes of scatter diagrams of number of ribs per whorl of Grey Shales species of *Dactylioceras* (*Orthodactylites*), plotted from 136 readings from 48 specimens of *D.* (*O.*) *semicelatum*, 104 readings from 45 *D.* (*O.*) *tenuicostatum* from bed 24, 89 readings from 37 from bed 22, 17 readings from 7 from bed 20, and 122 readings from 49 *D.* (*O.*) *clevelandicum* (total of 468 readings from 186 specimens).

average size of 18 complete adults from beds 22 and 24 is 88 mm diameter at the mouth border, the range being 72 to 105 mm, and there is no difference in the size range of specimens from the two beds. The length of the adult body chamber varies between 13/16 and 18/16ths of a whorl. The neotype (Pl. 5, fig. 1), from bed 22, is approximately average in adult size, length of body chamber and all whorl dimensions (Text-fig. 5); its rib-density is near to average for bed 22, and slightly less than average for bed 24, but well within the range of variation. One of the most densely ribbed specimens from bed 24 is figured in Pl. 6, fig. 2; it has 163 ribs on the whorl ending at 85 mm diameter, and a small portion of its final mouth border preserved at 90 mm diameter, the body chamber occupying 14/16ths of the final whorl. Another specimen from bed 24 is figured in Pl. 5, fig. 2, it being one of the least densely ribbed examples found at that horizon, and with an adult mouth border at 72 mm diameter, it is one of the smallest adults of the species.

In bed 20 specimens are less well preserved, and although 39 were collected, many are only fragments of whorls. None of them differ in whorl dimensions from *D.* (*O.*) *tenuicostatum* or from the more compressed part of the *clevelandicum* population. Their rib-densities are plotted as individual points on Text-fig. 6, and they can be seen to fall generally within or above the small range of overlap between those two species. A few are less densely ribbed than the bed 22 population, but some are considerably more densely ribbed than the bed 19*b* population, so, as there are no examples with depressed whorls, the bed 20 population is referred to *D.* (*O.*) *tenuicostatum*. The best specimen from bed 20 is figured in Pl. 6, fig. 3. The few specimens in bed 21 are typical fine-ribbed *D.* (*O.*) *tenuicostatum*, and the flat nodules of bed 26 contain a few moderately well-preserved, very fine-ribbed specimens similar to those of bed 24.

D. (*O.*) *tenuicostatum* is more densely ribbed than any of the other species described here, and has consistently slender and evolute whorls which are never depressed.

Dactylioceras (Orthodactylites) semicelatum (Simpson)

Pl. 6, fig. 1; Pl. 7, figs. 1, 2; Pl. 8, figs. 1–4; Pl. 9, figs. 1–3

1819 *Ammonites annulatus* J. Sowerby: 41, pl. 222, fig. 2 only (*non* Schlotheim, 1813).
1843 *Ammonites semicelatus* Simpson: 20.
1855 *Ammonites semicelatus* Simpson: 50.
1884 *Ammonites semicelatus* Simpson: 81.
1911 *Dactylioceras semicelatum* (Simpson) Buckman: pl. 31.
1927 *Kryptodactylites semicelatus* (Simpson) Buckman: pl. 31A.
1957 *Dactylioceras semicelatum* (Simpson) and spp.; Maubeuge: figs. 1–3, ? 18–21, 41, 42, 44, ? 46, 47, 48, ? 49, ? 58, ? 59 (1), 59 (2).
1957 *Dactylioceras pseudocrassoides* Maubeuge: 201, pl. 13, fig. 28.
1957 *Dactylioceras densicostatum* Maubeuge: 202, pl. 13, fig. 29.
1968 *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson); Hoffmann: 6, pl. 2, figs. 1, 2.
1968 *Dactylioceras* (*Orthodactylites*) *wunnenbergi* Hoffmann: 7, pl. 1, fig. 1.
1968 *Dactylioceras* (*Orthodactylites*) *eikenbergi* Hoffmann: 8, pl. 1, fig. 2.
1971 *Dactylioceras* (*Orthodactylites*) *anguinum* (Reinecke); Pinna & Levi-Setti: 90, pl. 2, figs. 1, 2, 5.
1971 *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson); Pinna & Levi-Setti: 90, pl. 2, figs. 3, 4, 15.

TYPE. The holotype is Whitby Museum no. 116, and was figured by Buckman (1911 : pl. 31). It is from bed 28 or 30 of the Grey Shales, and its locality is not known more accurately than "Whitby". Dimensions : at 80 mm diameter : 22·5 (0·28), ca. 17·5 (0·22), 40·5 (0·51) ; 69 ribs at 67 mm diameter, 56 ribs at 50 mm, 47 ribs at 36 mm.

DISTRIBUTION. Semicelatum Subzone. Grey Shales beds 28 to 32, from which 102 specimens were collected.

DIAGNOSIS. Whorls about one-quarter involute, moderate whorl height, moderate to wide umbilicus, whorl section elliptical with narrow venter in compressed forms, where whorl breadth is less than height, but rounded in depressed whorls, where breadth/height ratio is up to 1·8 at 50 to 70 mm diameter. Ribs straight, rectiradiate or prorsiradiate, single or bifurcating, moderate to low variable rib-density. Small ventro-lateral tubercles on depressed whorls. Adult body chamber more compressed than earlier whorls, with more single ribs and no tubercles. Adult size 75 to 120 mm diameter, adult body chamber occupies 11/16 to 14/16ths of a whorl.

DESCRIPTION. A small proportion of the nodules in bed 28 contain single specimens of *D.* (*O.*) *semicelatum.* The preservation is only moderately good, and the nodules are extremely hard with much pyritization of and around the ammonites, so that specimens are difficult to extract. They are usually large and fully grown, but occasionally several small examples are found in one nodule. The nodules of bed 30 are even harder and there is more pyritization, but ammonites occur in more of the nodules and are better preserved. When the nodules have been subjected to foreshore weathering they will crack along the surface of the ammonites, and a larger collection was obtained from bed 30, including some very well-preserved complete adults. From about the middle of bed 31 up to 0·30 m below the top of bed 32, crushed specimens occur commonly, especially in patches in the shell beds at the base of bed 32. A small pyritic mass in bed 32 contained several small solid inner whorls and fragments.

D. (*O.*) *semicelatum* is about one-quarter involute and has relatively high whorls, with a characteristic elliptical whorl section in many specimens. This whorl shape occurs in the more compressed individuals where the whorl breadth is greatest near the umbilicus, and decreases towards a narrowly rounded venter. There is a large amount of variation in whorl breadth, especially on the inner whorls, for all gradations are found between slender compressed whorls, in which the breadth/height ratio is about 0·8 at 50 mm diameter, to greatly depressed coronate whorls in which the ratio is as high as 1·8 at a similar size. In adult whorls the variation is much less, because specimens with depressed inner whorls become less depressed on the final whorl, where whorl breadth and height are almost equal. Rib-density is generally moderate, but is highly variable on inner whorls depending on the whorl shape. Compressed inner whorls have moderately dense ribs, while depressed inner whorls have a much lower rib-density. The rib-density variation for 48 specimens from beds 28 and 30 is shown in Text-fig. 5. Points are evenly scattered over the area of variation in that diagram. On depressed inner whorls ventro-lateral tubercles are formed. No differences could be detected between the populations of beds 28 and 30. Fourteen complete adults have mouth diameters varying between 77 and 117 mm (average 94 mm), and the length of the body chamber varies between 11/16 and 14/16ths of a whorl.

A large complete adult from bed 30 with compressed whorls throughout and average rib-density is figured in Pl. 7, fig. 1. Another complete adult from the same bed figured in Pl. 9, fig. 1 has depressed, sparsely ribbed inner whorls, changing to a more compressed, more densely ribbed outer whorl. The inner whorls of four specimens from bed 30 are shown in Pl. 8, figs. 1–3 and Pl. 9, fig. 2 to illustrate the amount of variation in whorl shape and rib-density. The two end members of the series are very different, yet all intermediates occur between them. Two examples from bed 28 are illustrated : one, Pl. 6, fig. 1, is a normal compressed type with moderately dense ribs, while the other, Pl. 7, fig. 2, has only slightly fewer ribs, but has a much greater whorl breadth.

The crushed specimens throughout much of the thickness of beds 31 and 32 show the characters of *D.* (*O.*) *semicelatum* fairly clearly. Whorl thicknesses cannot be observed, but some specimens, such as that figured in Pl. 8, fig. 4 from the middle of bed 31, show clearly inner whorls with few ribs, small ventro-lateral tubercles and an original depressed whorl shape that is now crushed, changing to a high more compressed outer whorl with many more ribs. A specimen with average rib-density and probably with originally compressed whorls from the shell bed at the base of bed 32 is figured in Pl. 9, fig. 3.

D. (*O.*) *semicelatum* is more involute and has higher whorls than either *tenuicostatum* or *clevelandicum*. Differences between *semicelatum* and *crosbeyi* are less and there is some overlap in the variation of the two. *D.* (*O.*) *crosbeyi* as a whole is more involute, has higher whorls and is not as compressed as *semicelatum*, and it does not have the characteristic elliptical whorl shape and narrow venter. The extremely depressed variants of *crosbeyi* have much broader whorls than *semicelatum*. The adult body chambers of *crosbeyi* are shorter than any in *semicelatum* ; this is probably a reflection of the usually stouter whorls of the former.

The widespread distribution of *D.* (*O.*) *semicelatum* in eastern France, Luxembourg and north-west Germany is described in detail in the section on correlation (pp. 268–270). A typical densely ribbed specimen was figured as the new species *D. densicostatum* by Maubeuge (1957 : fig. 29) and another specimen (fig. 28) with a large whorl breadth and distant ribs, almost exactly like the inner whorls of Pl. 9, fig. 1, was made the type of *D. pseudocrassoides*. Two specimens from north-west Germany with larger than average whorl breadth and ribs of fairly low density were made the types of *D. wunnenbergi* and *D. eikenbergi* by Hoffmann (1968) ; both can be matched with specimens from bed 30 of the Grey Shales, and they are synonyms of *D. semicelatum*.

Family **HILDOCERATIDAE** Hyatt, 1867

The two Hildoceratid ammonites found in the Grey Shales are *Protogrammoceras paltum* (Buckman) in bed 3 and *Tiltoniceras antiquum* (Wright) in bed 32, both belonging to the subfamily Harpoceratinae. These species will be described in detail in another paper, so only a short account of their occurrence and identification is given here.

Protogrammoceras paltum (Buckman)

1922 *Paltarpites paltus* Buckman : pl. 362A.
1923 *Paltarpites paltus* Buckman : pl. 362B.
1964 *Paltarpites paltus* Buckman ; Maubeuge & Rioult : 107–113, 6 figs.
1966 *Paltarpites paltus* Buckman ; Maubeuge & Rioult : 305–308, 3 figs.

DISTRIBUTION. Paltum Subzone. Grey Shales bed 3, from which four specimens were obtained and the impressions of two further large specimens were seen.

DESCRIPTION. Two of the specimens collected are large and well preserved, and consist of one whole whorl, half septate and half body chamber in each case, with all the smaller whorls missing, and the final part of the body chamber missing. C.47972 from Runswick Bay has a maximum size of 175 mm diameter; C.72521 from Hawsker Bottoms is 140 mm diameter. The other two specimens are poorly preserved: C.77262 from Hawsker Bottoms is crushed and has about three whorls up to about 100 mm diameter; C.77296 from east Kettleness is a fragment of a small section of a whorl at about 180 mm diameter. In addition two poorly preserved external moulds seen in bed 3 at east Kettleness and Holmsgrove Sand were both about 200 mm diameter. This is probably the approximate size of complete adult specimens, for both the well-preserved specimens would have been about that size when complete. These Grey Shales specimens agree exactly with the holotype of *P. paltus* (Buckman 1922 : pl. 362A) which comes from layer P of the Junction Bed at Thorncombe Beacon, Dorset. A paratype from the same bed and locality (Buckman 1923 : pl. 362B) shows somewhat coarser ribs on the inner whorls, while a specimen from the Marlstone Rock Bed at South Petherton, Somerset (Buckman 1923 : pl. 363) has finer ribbing throughout but is probably conspecific. The examples from Luxembourg described by Maubeuge & Rioult (1964; 1966) are also exactly like the Dorset and Yorkshire specimens, and attain a size of 150 mm diameter about half-way along the body chamber.

Comparison of the holotype of *Paltarpites paltus* with the lectotype of *Protogrammoceras bassanii* (Fucini 1901 : 46, pl. 10, figs. 6*a–c*), the type species of *Protogrammoceras*, shows that there are no differences worthy of generic distinction, and so *Paltarpites* is a synonym of *Protogrammoceras*.

Tiltoniceras antiquum (Wright)

1875 *Ammonites acutus* Tate : 204 (*non* J. Sowerby, 1813).
1882 *Harpoceras antiquum* Wright : pl. 57, figs. 1–4.
1883 *Harpoceras antiquum* Wright : 431.
1884 *Harpoceras acutum* (Tate) Wright : 469, pl. 82, figs. 7, 8.
1887 *Ammonites acutus* Tate ; Denckmann : 59, pl. 10, figs. 1–3.
1887 *Ammonites capillatus* Denckmann : 60, pl. 1, fig. 7 ; pl. 4, fig. 3.
1893 *Harpoceras schroederi* Denckmann : 110.
1913 *Tiltoniceras costatum* Buckman : *viii*.
1914 *Tiltoniceras costatum* Buckman : pl. 97, figs. 1–4.

Distribution. Upper part of the Semicelatum Subzone. Abundant in bed 32, especially in two shell beds at the base, and about 450 specimens were collected, mainly as crushed groups attached to slabs of shale.

Description. The majority of the specimens in the shell beds are between 20 and 30 mm diameter, some are up to 50 mm, but only a few are larger, and the largest found is 100 mm diameter. Most have at least part of their body chambers, so in view of the much larger sizes attained by isolated specimens, the shell beds probably consist of immature specimens of 20 to 50 mm diameter. There is no evidence that any of them are adult. Though crushed, a number can be seen to have smoothly rounded, not angled, umbilical edges, especially in one specimen where a small part is pyritized and uncrushed. Only two larger specimens are known in Yorkshire. The one figured by Wright (1882 : pl. 57, figs. 1–4) as the holotype of *T. antiquum* is a magnificent specimen about 190 mm diameter at the final mouth border, in which the septate whorls are crushed flat, and the body chamber is preserved solid and shows the rounded umbilical edge well. It came from Hawsker Bottoms. The second large specimen (C.50353) was collected by myself about 0·45 m below the top of bed 32 at east Kettleness, and consists of most of a well-preserved solid body chamber, 130 mm diameter, also showing a smoothly rounded umbilical edge. This is the only feature that distinguishes *Tiltoniceras* from *Eleganticeras*, its successor in the Exaratum Subzone, which always has an angled umbilical edge.

The population of *Tiltoniceras* in the Transition Bed of the Midlands is exactly the same in morphology, and also consists largely of small immature specimens, with only very rare large adults. The specific name *Ammonites acutus* Tate, 1875, applied to them is pre-occupied by *A. acutus* J. Sowerby, 1813, so *Tiltoniceras antiquum* is the first available name for the species. *T. costatum* Buckman (1913), given to an individual with stronger ribs, is a synonym, for the rib strength and density shows a moderate amount of variation.

The synonymy given above is not complete. Only the English and first-described north-west German occurrences are listed. More recent descriptions of the German fauna and occurrences in north-east Siberia are discussed below in the section on correlation.

IV. ZONAL SUBDIVISIONS

The history of the nomenclature and synonymy of the Tenuicostatum Zone was discussed by Dean, Donovan & Howarth (1961 : 476). Briefly, the zone was introduced as the "Zone of *Ammonites annulatus*" by Tate & Blake (1876 : 168), and altered to the Zone of *Dactylioceras tenuicostatum* by Buckman (1910*a* : 85) who realized that Tate & Blake had mis-identified the index species. That index species was the ammonite known to Tate & Blake to be very common at about the middle of the Grey Shales. So the Yorkshire coast and the Grey Shales are the type area and formation for the Tenuicostatum Zone. Ammonites of the subgenus *Orthodactylites* are characteristic of the zone, particularly the index species and the closely related *O. semicelatum*, which is now known to occur at a higher horizon. In the Midland counties of England the Transition Bed overlies the

Marlstone Rock Bed, and contains two ammonites commonly, *Dactylioceras* (*Orthodactylites*) *directum* (Buckman) and *Tiltoniceras* (*T. acutum* (Tate) and *T. costatum* Buckman, both now held to be synonyms of *T. antiquum* (Wright)). These Transition Bed ammonites were the basis of the *acutum* hemera of Buckman (1898 : 450, table 1), the Acutum Zone of Walford (1899 : 33), and the *directus* and *Tiltoniceras* hemerae of Buckman (1930 : 41). The Transition Bed immediately overlies the Marlstone Rock Bed, which is traditionally of Spinatum Zone age because of the occasional occurrence of *Pleuroceras*, so *Tiltoniceras* and *D.* (*O.*) *directum* were thought to be the earliest ammonites of the Tenuicostatum Zone by Dean, Donovan & Howarth (1961 : 476), and indeed the zone had been divided into a lower *Tiltoniceras acutum* Subzone and an upper *Dactylioceras tenuicostatum* Subzone by Arkell (1933 : 165 ; 1956 : 35). A similar sequence has recently been used in France, where the Tenuicostatum Zone has been divided into a lower " Tiltoniceras " Subzone and an upper Semicelatum Subzone (Mouterde *et al.* 1971 : 82). But *Tiltoniceras* is now known to occur in the top part of the Yorkshire Grey Shales at the same level as *D. semicelatum* and above *D. tenuicostatum*, so the Transition Bed of the English Midlands belongs to the highest part of the Tenuicostatum Zone. It is not proposed to perpetuate the use of a species of *Tiltoniceras* as a subzonal index, because the species *acutum*, always used before, is pre-occupied and has to be replaced by *antiquum*, and *Tiltoniceras* is probably less widespread than the accompanying *D. semicelatum*, which is likely to prove a more useful index species.

On the basis of the sequence of ammonites found in the Yorkshire Grey Shales, the following four subzones are proposed for the Tenuicostatum Zone :

(Top)	Subzone of *Dactylioceras* (*Orthodactylites*) *semicelatum*
	Subzone of *Dactylioceras* (*Orthodactylites*) *tenuicostatum*
	Subzone of *Dactylioceras* (*Orthodactylites*) *clevelandicum*
(Bottom)	Subzone of *Protogrammoceras paltum*

The top of the Tenuicostatum Zone is drawn (as explained above, p. 239) to coincide with the top of the Grey Shales in Yorkshire, that is between the highest *D. semicelatum* and *Tiltoniceras* 0·30 m below the top of bed 32, and the appearance of *Eleganticeras* in bed 33 ; in fact the boundary is placed at the base of bed 33. The bottom of the Tenuicostatum Zone poses more difficult problems in Yorkshire because there are very few ammonites low in the zone. It has to be above the highest *Pleuroceras*, which is characteristic of the Spinatum Zone, and in a previous paper it was placed at a convenient lithological boundary, the top of the Ironstone Series (top of Kettleness bed 28, Howarth 1955 : 156). Later work by Hallam (1967 : 403) and Chowns (1966 ; and personal communication), mainly on the lithology, has suggested that the base of Kettleness bed 26, the " Sulphur Band ", is a better base for the zone. This is above the highest *Pleuroceras* in bed 25 and marks a persistent and distinctive lithological change. It is now known that the single specimen of *Dactylioceras* (*D.*) *pseudocommune* from north-west Cleveland probably came from the Top Main Dogger, the next bed above the " Sulphur Band " and the top bed of the Ironstone Series, being probably equivalent to Kettleness beds 27 and 28 on the coast. This species belongs to the earliest group of *Dactylioceras* that mark the base of the Tenuicostatum Zone in Italy, and the base of the zone in Yorkshire is drawn, therefore, at the bottom of the " Sulphur Band " (Kettleness bed 26) between the highest *Pleuroceras* and the lowest *Dactylioceras*, at a distinctive lithological change which is also the horizon of a non-sequence in north-west Cleveland (Chowns 1966 : fig. 1). It is of interest that this specimen of *Dactylioceras* occurs in a bed that is equivalent to a horizon (bed 27) only about 0·60 m above *Pleuroceras hawskerense* at Kettleness, so that the earliest group of *Dactylioceras* to which it belongs can be shown to follow closely above the last *Pleuroceras* in Yorkshire.

The Paltum Subzone is proposed for the lowest part of the Tenuicostatum Zone, which in Yorkshire and several areas of south-west England contains large specimens of *Protogrammoceras paltum*. *Dactylioceras* is very rare at this level in England, and in practice the base of the subzone (and the zone) has to be drawn above the highest *Pleuroceras* of the Spinatum Zone. *Dactylioceras* (*Orthodactylites*) appears in force in Yorkshire at the base of the Clevelandicum Subzone, first with *D.* (*O.*) *crosbeyi*, followed by *D.* (*O.*) *clevelandicum*. This subzone has not so far been identified outside Yorkshire. The Tenuicostatum Subzone is marked by the range of the index species, *D.* (*O.*) *tenuicostatum*, a highly distinctive ammonite of widespread occurrence in England and elsewhere. The Semicelatum Subzone is similarly drawn to coincide with the range of its index species *D.* (*O.*) *semicelatum*, also a distinctive ammonite of widespread occurrence. The other common British *Orthodactylites, D.* (*O.*) *directum*, occurs in both the Tenuicostatum and Semicelatum Subzones in the Midlands and south-west England. *Tiltoniceras* occurs in the upper part of the Semicelatum Subzone in Yorkshire, but its distribution within the subzone is not known in other areas.

V. CORRELATION WITH OTHER AREAS

ENGLAND. The occurrence and subdivision of the Tenuicostatum Zone in other parts of England will be described in another paper. Comment here is confined to the observation that the Transition Bed of the Midlands belongs to the Semicelatum Subzone, and that the top part (? up to 1 m) of the Marlstone Rock Bed belongs to the Tenuicostatum Subzone.

NORTH-WEST GERMANY. The subdivisions proposed by Denckmann (1893) and other workers were summarized by Dean, Donovan & Howarth (1961 : 477, 479). Later work by Hoffman & Martin (1960), Hoffmann (1960 : 75, 76 ; 1968) and Lehmann (1968), including data from boreholes, has established that the zone is up to 7·5 m thick. Two rows of nodules occur, the Capillatum Nodules (after *Tiltoniceras capillatum* (Denckmann)) at the top, and the Siemensi Nodules (after *Lytoceras siemensi* (Denckmann)) 0·5–1·0 m below. From these Hoffmann (1968 : 21) derived two divisions of the Tenuicostatum Zone, the Capillatum Subzone above and the Siemensi Subzone below. Lehmann (1968 : 63) pointed out that *L. siemensi* also occurs in the Exaratum Subzone and is therefore unsuitable as an index species, and he combined the two into the Siemensi-Capillatum (="Acutum ") Subzone.

The following ammonites from the two rows of nodules have been figured, mainly under different specific names, all of which are considered to be synonyms of the species indicated below:

Capillatum Nodules:

Tiltoniceras antiquum—Hoffmann 1968: pl. 4, fig. 3; pl. 5, figs. 2, 3.

Dactylioceras (*Orthodactylites*) *semicelatum*—Hoffmann 1968: pl. 2, fig. 2.

D. (*O.*) *directum*—Hoffman 1968: pl. 2, figs. 3, 4; pl. 3, fig. 1 (refigd. Lehmann 1968: 46, pl. 17, fig. 6).

Siemensi Nodules:

Tiltoniceras antiquum—Hoffmann 1968: pl. 3, fig. 4; pl. 4, figs. 1, 2; pl. 5, figs. 1, 4.

Dactylioceras (*Orthodactylites*) *semicelatum*—Hoffmann 1968: pl. 1, figs. 1, 2 (examples with thick whorls); pl. 2, fig. 1.

D. (*O.*) *directum*—Hoffmann & Martin 1960: pl. 9, fig. 5; pl. 10, figs. 2a, 2b.

Lytoceras siemensi—Hoffmann & Martin 1960: pl. 10, fig. 1.

Tiltoniceras antiquum, *D.* (*O.*) *semicelatum* and *D.* (*O.*) *directum* occur in both rows of nodules, so they both belong to the Semicelatum Subzone, when compared with the succession now known from Yorkshire and with the ammonites in the Midlands Transition Bed. No definite specimens of *D.* (*O.*) *tenuicostatum* are known from the shales below the nodules. Some of the ammonites from the top 1·5 m of the 6·4 m of shales belonging to the Tenuicostatum Zone in the borehole were figured by Hoffmann & Martin (1960: pl. 8, figs. 1–3; pl. 9, figs. 1–4) as *D.* (*O.*) *tenuicostatum*. They are all crushed and difficult to determine, but some appear to have the high whorls of *D.* (*O.*) *semicelatum*. Thus, all the Tenuicostatum Zone ammonites known so far in north-west Germany belong to the highest subdivision, the Semicelatum Subzone.

EASTERN FRANCE AND LUXEMBOURG. The development of the Tenuicostatum Zone has been described by Maubeuge (1948; 1952). The zone consists of shales and marls, with some limestone, and is thin (up to 1 m) in most places, but at Bettembourg, Luxembourg, a good section is exposed in two quarries and the zone is 4·9 m thick. The Dactylioceratidae were described in another paper by Maubeuge (1957), and in the following section of the beds at Bettembourg, the ammonites are my determinations of Maubeuge's figures:

(Shales, bituminous; impressions of "*Dactylioceras* cf. *semicelatum*" at the base).

3 Shale, marly, closely laminated, 2·60 m.

Dactylioceras semicelatum (figs. 16, ? 18–21, 29, ? 58, ? 59 (1)).

D. directum (figs. 9 (2–5), 14, 24, 25, 27, 38, 52–56).

Dactylioceras sp. indet. (figs. 9 (1), 17, 22, 23, 26, 36, 37, 39, 45, 57, 62, 63).

2 Limestone, 0·50 m.

Dactylioceras directum (fig. 15).

D. semicelatum (fig. 41).

1 Shale, marly, 1·80 m.

Protogrammoceras paltum (Maubeuge & Rioult 1964; 1966).

Bed 3 belongs to the Semicelatum Subzone and contains several typical examples of the index species and of *D. directum*—the holotype of *D. densicostatum* Maubeuge (1957, fig. 29) is a typical *D. semicelatum*, the holotypes of *D. semicelatoides* (fig. 27) and *D. microdactyliformis* (fig. 38) belong to *D. directum*, while the holotypes of *D. obliquecostatum* (fig. 36) and *D. mastodontoides* (fig. 57) are not specifically determinable. The limestone of bed 2 also appears to belong to the Semicelatum Subzone because of a *D. directum* (fig. 15) and a *D. semicelatum* (fig. 41—the whorl height is much too large for *D. tenuicostatum*) which it contains. *Protogrammoceras paltum* occurs at the base of bed 1 (Maubeuge & Rioult 1964 : 112, footnote), and the three crushed specimens and the fragment of a large well-preserved body chamber that were figured by Maubeuge & Rioult (1964 ; 1966) agree exactly with those found in bed 3 of the Yorkshire Grey Shales. The base of bed 1 at Bettembourg can be referred to the Paltum Subzone. Ammonites of the Clevelandicum and Tenuicostatum Subzones have not been found.

The following ammonites from other areas were also figured by Maubeuge (1957):

Dactylioceras semicelatum—figs. 1–3, 8, 28, 42, 44, ? 46, 47, 48, ? 49, 59 (2).

D. directum—fig. ? 43.

D. ? *crosbeyi*—figs. ? 6, ? 7.

Dactylioceras sp. indet.—figs. 4, 5, 10–13, 30–35, 40, 50, 51, 60, 61.

These include the holotype of *D. pseudocrassoides* (fig. 28) from Bourmont (Haute Marne), which agrees closely with the broad, distantly ribbed inner whorls of some specimens of *D. semicelatum* such as that figured in Pl. 9, fig. 1 from bed 30 of the Yorkshire Grey Shales. Two other specimens of *D. semicelatum* from Bourmont were also figured (figs. 8, 59 (2)). The type specimens of the two new species *D. novimagense* (fig. 35) and *D. lamellosum* (figs. 50, 51) are specifically indeterminate.

Finally two further new specific names are difficult to place : the holotypes of *D. pseudosemicelatum* (fig. 6) and *D. podagrosum* (fig. 7) are both from Audeloncourt (Haute Marne) and appear to be conspecific. All the other figured ammonites from Audeloncourt (figs. 4, 5, 60) are indeterminate, and give no indication of age. These two holotypes have broad whorls but no ventro-lateral tubercles ; they might be examples of *D. crosbeyi*, and if this determination could be confirmed by better and larger specimens, it would be the only record of that species and of the Clevelandicum Subzone outside Yorkshire.

The records summarized above show that in eastern France and Luxembourg there is good evidence of the Semicelatum Subzone at many localities, the Paltum Subzone occurs at Bettembourg, the Clevelandicum Subzone may occur at one locality, but no evidence of the Tenuicostatum Subzone has yet been found.

AUSTRIA AND ITALY. The earliest known *Dactylioceras* are the four species *D.* (*D.*) *pseudocommune* and *simplex*, and *D.* (*Orthodactylites*) *mirabile* and *polymorphum*, all of Fucini (1935), first described from Taormina, Sicily, and assigned by him to the Domerian (Upper Pliensbachian). Their nomenclature was revised by Pinna & Levi-Setti (1971 : 89–91), who also described examples from northern Italy, but without adding any stratigraphical data. More specimens from central and northern Italy were described by Cantaluppi & Savi (1968 : 231) who claimed to have determined their age as Upper Domerian, and by Ferretti (1967 ; 1970) who found them in a stratigraphical sequence marking the base of the Toarcian. Ferretti's evidence was that in two different areas the *Dactylioceras* fauna occurred only above faunas of *Emaciaticeras* and *Canavaria* which were typical of the top part of the Domerian, and the Domerian–Toarcian boundary could be accurately drawn between them. Specimens of *Protogrammoceras* (determined as "*Mercaticeras*" by Ferretti) accompanied the *Dactylioceras* and it was similar specimens that had led Cantaluppi & Savi (1968) to date their fauna as Domerian, but it is well known that *Protogrammoceras* ranges up as far as the top of the Tenuicostatum Zone. The sequence of ammonite faunas in the top half of the Domerian in the Mediterranean area that was used by Ferretti is best shown in Portugal (Mouterde 1967 : 216–217) and Morocco (Dubar 1954 : 24), where the following succession has been established :

4 *Dactylioceras* and *Protogrammoceras*. Base of Toarcian, Tenuicostatum Zone.

3 Horizon with *Canavaria* (including "*Taurommeniceras*"), *Protogrammoceras* and *Pleuroceras spinatum*.

2 Horizon with *Emaciaticeras, Canavaria* and *Protogrammoceras*.

1 Horizon with *Lioceratoides, Protogrammoceras, Pleuroceras solare* and *P. spinatum*.

Horizons 1–3 represent the Spinatum Zone of the north-west European Province because *Pleuroceras* occurs at most levels in Portugal, and they do not represent ammonite faunas that occur between the typical north-west European *Pleuroceras* and *Dactylioceras* faunas, as claimed by Ferretti (1970 : 456).

The ammonites from Taormina, Sicily, that were described by Fucini, were existing museum specimens obtained mainly from screes without knowledge of their stratigraphical relationships. Fucini referred them all to the Domerian substage, an age assessment that was questioned by Arkell (1956 : 210) who thought that the Dactylioceratidae were probably Toarcian. The most readily obtainable Taormina ammonites do come from screes, but some forms can be collected *in situ*, as was found when the author collected there in 1957. In fact three faunas were collected from single beds :

1 From a limestone 0·20 m thick in a quarry east of the Fontanelle ravine—*Arieticeras naxense* (Gemmellaro), *Emaciaticeras lottii* (Gemm.), *E. timaei* (Gemm.), *Fontanelliceras fontanellense* (Gemm.), *F. juliae* (Bonarelli), *Canavaria haugi* (Gemm.), *C. canavarii* (Gemm.) and *Protogrammoceras hoffmanni* (Gemm.). This is a rich mixed fauna of Hildoceratidae from horizon 2, the *Emaciaticeras* horizon.

2 From a marly limestone 0·30 m thick in the Fontanelle ravine—*Pleuroceras solare* (Phillips) (abundant), *P. spinatum* (Bruguière) and *Lioceratoides aradasi* Fucini. This association can be dated as horizon 1 from the presence of *Lioceratoides*, and the many specimens of *Pleuroceras solare* show that horizon 1 is equivalent to the Apyrenum Subzone of the Spinatum Zone of north-west Europe. This is probably the bed from which some of Fucini's (1924 : pl. 1, figs. 5, 6, ? 3) specimens of *Pleuroceras* were obtained. Thus it can be shown again that the *Lioceratoides* horizon is not younger than the *Pleuroceras* faunas of north-west Europe.

3 From a marly limestone 0·15 m thick at Tirone Cliff, stratigraphically high in the succession—*Dactylioceras* (*D.*) *pseudocommune* Fucini and *D.* (*Orthodactylites*) *polymorphum* Fucini. It is significant that there were no accompanying ammonites with this, the only collection of *Dactylioceras* found *in situ*, and it can be concluded that, as in central and northern Italy, the earliest fauna of *Dactylioceras* occurs at a higher level than the typical Domerian Hildoceratidae, and that it marks the base of the Tenuicostatum Zone at the bottom of the Toarcian.

A similar fauna occurs at Kammerker, Austria, and has been described by Fischer (1966), who proposed the new specific name *D. triangulum* for specimens that are a close match for *D. pseudocommune*. *D. semicelatum* probably occurs higher in the Tenuicostatum Zone in Italy, for six specimens figured by Pinna & Levi-Setti (1971 : 90, pl. 2, figs. 1–5, 15) seem to belong to that species, but the Kammerker specimen figured as *D. semicelatum* by Fischer (1966 : 21, pl. 3, fig. 4) is a small indeterminate fragment.

PORTUGAL, SPAIN AND NORTH AFRICA. The Tenuicostatum Zone is probably well represented in Portugal and might attain a thickness of as much as 30 m. The occurrences are summarized by Mouterde (1967 : 218) and several species of *Dactylioceras*, including *D. semicelatum*, are recorded. None are figured, nor are the accompanying Hildoceratidae determined as *Ovaticeras* cf. *ovatum*, *Eleganticeras* " *elegans* " (Y. & B.) and *Harpoceras capellinum*, all of which are post-Tenuicostatum Zone forms. Until the whole of this ammonite fauna is figured accurate assessment of the age is not possible. The zone is probably present in Spain, and descriptions that include records that might be Tenuicostatum Zone Dactylioceratidae were given by Behmel & Geyer (1966), Dubar, Elmi & Mouterde (1970) and Mouterde (1970). An occurrence of the Tenuicostatum Zone in Morocco with *Dactylioceras* has been recorded by Dubar (1954 : 23).

The ammonite *Bouleiceras* occurs rarely in the Tenuicostatum Zone of Portugal and Spain, and also in Morocco. These are occurrences outside the main area for the *Bouleiceras* assemblage in West Pakistan, Arabia and east Africa, where species of *Protogrammoceras*, especially *P. madagascariense* (Thevenin), are the usual accompanying ammonites. The distribution of this assemblage is described in another paper (Howarth 1973). No Dactylioceratidae are known from the assemblage, and the age assessment is based on the presence of *Bouleiceras* in Portugal, and the presence of *Protogrammoceras*, which is known in the Tenuicostatum Zone, but not higher, in several areas of Europe.

EASTERN EUROPE. The occurrence of the Tenuicostatum Zone in Bulgaria has been summarized by Sapunov (1968 : 140), and ammonites identified as *D. tenuicostatum*, *D. semicelatum* and *D. acanthus* were figured in an earlier paper (Sapunov 1963 : 116–118, pl. 1, figs. 1–4). These come from a locality where the Tenuicostatum, Falciferum and Bifrons Zones occur in a condensed bed only 0·42 m thick. Although one of the figured specimens (Sapunov 1963 : pl. 1, fig. 3) does appear to be a *D. semicelatum*, identification of Dactylioceratidae from condensed deposits is extremely difficult and uncertain. Records of species of *Tiltoniceras* from the same condensed beds are not supported by figured specimens, but if correct they would prove to be an interesting easterly extension of the range of the genus, at present known only from England and north-west Germany in Europe.

No Tenuicostatum Zone ammonites have been found in Hungary. The presence of the Tenuicostatum Zone in Romania is shown by seven ammonites from the Brasov area figured by Popa (1970 : 90, figs. 1–7). The preservation is only moderate, and all could be examples of *D. semicelatum*, indicating the highest part of the zone, but one (Popa 1970 : fig. 1) might be a *D. tenuicostatum*, showing that a lower horizon may be present as well.

NORTH-EAST SIBERIA. The Upper Lias is well developed and rich in ammonites in the basin of the Omolon River (lat. 65° N, long. 161° E) especially in the area of its tributary, the River Kedon. Beds belonging to the Tenuicostatum Zone are shales with nodules up to 15–18 m thick; they overlie beds with late species of *Amaltheus*, probably of the Spinatum Zone, and are overlain by beds that contain good specimens of *Harpoceras exaratum* (Polubotko & Repin 1966 : pl. 1, fig. 7; Repin 1968 : pl. 45, figs. 2–4, pl. 47, fig. 1) indicating the Exaratum Subzone. The stratigraphy was first described by Dagis & Dagis (1965 : 15) who recorded *Ovaticeras propinquum* (Whiteaves), *Catacoeloceras* spp. and ? *Mercaticeras* from several levels within the 15 m of beds for which the term " Zone of *Ovaticeras propinquum* " was proposed. More localities were described the following year by Polubotko & Repin (1966 : 30), and examples of the " *Ovaticeras* " described and figured as a new species, *O. facetum* Polubotko & Repin (1966 : 45, pl. 1, figs. 4, 5, 8), came from the upper one-third of the zone. The zonal term was replaced by the " Zone of *Ovaticeras facetum* ". More specimens of *O. propinquum* and *O. facetum* from the Omolon area were figured later by Repin (1968 : 115, 116, pl. 44, fig. 1; pl. 45, fig. 1, pl. 46, figs. 1, 2), together with two specimens identified as *Tiltoniceras* sp. (Repin 1968 : 116, pl. 44, figs. 2, 3). These two species of " *Ovaticeras* " contain some very well-preserved specimens up to 90 mm diameter, and the figured ones are all undoubted examples of *Tiltoniceras* that do not seem to differ from the English species *T. antiquum*. In fact precise matches for them can be found amongst the fauna of *T. antiquum* in the Transition Bed at Tilton, Leicestershire. [" *Ovaticeras* " *propinquum* (Whiteaves) is a *Harpoceras* from the Lower Toarcian (? Falciferum Zone) of British Columbia.] The specimens figured by Repin as *Tiltoniceras* sp. are more heavily ribbed, and do not appear to differ from the typical *Harpoceras exaratum* microconchs figured by Repin (1968 : 117, pl. 45, figs. 2, 3) from the Exaratum Subzone.

A highly depressed Hildoceratid ammonite, that was probably the form recorded as ? *Mercaticeras* by Dagis & Dagis (1965), was described as the new genus *Arctomercaticeras* by Repin (1968*a*), which is here considered to be one of the last genera of the subfamily Arieticeratinae. The Dactylioceratidae from the Tenuicostatum Zone of the Omolon Basin were described by Dagis (1968 : 56–62, pl. 11, figs. 1–7) as two species of his new genus *Kedonoceras*. They came from near the base of the zone, well below the main occurrence of *Tiltoniceras*, and the genus was proposed for the depressed whorl shape, the presence of ventro-lateral tubercles, and the form of the suture-lines that largely reflect the cadicone shape of the shell. These depressed forms are exactly like those found in all the Yorkshire Grey Shales species except *D. tenuicostatum*. Depressed specimens of *D. crosbeyi* from bed 18 such as those in Pl. 2, figs. 1, 3 compare very closely with *Kedonoceras comptum* Dagis (1968*a* : pl. 11, figs. 1, 2), and the generic name *Kedonoceras* could equally well be applied to the Yorkshire forms. For reasons given earlier the Yorkshire depressed forms are thought to be part of the variation within species of *Dactylioceras* (*Orthodactylites*), and it seems that *Kedonoceras* might well be placed in synonymy, even if the Siberian forms are specifically different, because some considerably less depressed forms occur as well (e.g. Dagis 1968 : pl. 11, fig. 4).

The dating of *Tiltoniceras* as late Tenuicostatum Zone is confirmed, therefore, in north-east Siberia, where the Tenuicostatum Zone up to 18 m thick contains *Tiltoniceras* in the top one-third, indicating the Semicelatum Subzone, and depressed forms of *Dactylioceras* (*Orthodactylites*) near the base that closely resemble those occurring in the Clevelandicum Subzone.

WESTERN NORTH AMERICA. Small ammonites from the South Barrow borehole in north Alaska were figured as *Dactylioceras* cf. *semicelatum* and *D.* cf. *kanense* McLearn by Imlay (1955 : 87, 88, pl. 10, figs. 6, 13, 14). They could well be Tenuicostatum Zone forms, but are somewhat small for definite identification. The Maude Formation of Skidegate Inlet, Queen Charlotte Islands, British Columbia, contains *Dactylioceras kanense* McLearn (1932 : 59, pl. 4, figs. 1–7 ; pl. 5, figs. 6–9), which probably occurs at the same horizon as *Harpoceras propinquum* (Whiteaves) and *H. allifordense* McLearn. It is not possible to date this fauna in terms of European zones, although the two species of *Harpoceras* probably indicate the Falciferum Zone rather than the Tenuicostatum Zone. *D. kanense* is probably an *Orthodactylites*, judging from the rib pattern of the holotype (refigured Frebold 1964 : pl. 7, fig. 4 ; Imlay 1968 : pl. 3, fig. 12) and could be of Tenuicostatum Zone or Exaratum Subzone age. Age determinations are even more difficult for a series of Dactylioceratidae from Eastern Oregon and California figured mainly as various species of *Orthodactylites* by Imlay (1968 : 30–32, pl. 3, figs. 1–16). Some of them (figs. 13–16) appear to have the tuberculation pattern of *Prodactylioceras*, but others (figs. 1, 2, 8, 11) have all the characters of *Orthodactylites*. The ammonite *Fanninoceras* occurs in the Nicely Shale Formation at or above the horizon of some of these *Dactylioceras*, and in view of the fact that *Fanninoceras* is now interpreted as a Lower Pliensbachian Oxynoticeratid, it seems that a re-assessment of the occurrence and age of all the ammonites in this formation is required. In particular, a ? *Dactylioceras* with widely spaced ribs (Imlay 1968 : pl. 3, figs. 3–6) and *Fanninoceras* (pl. 8, fig. 21) come from the same locality, though their relative stratigraphical positions are not recorded. The genus *Arieticeras*, a typical Margaritatus and Spinatum Zone form, accompanies many of these ? *Orthodactylites* and ranges almost to the top of the Nicely Shale. If the association of genuine *Arieticeras* and *Orthodactylites* could be confirmed, and dated as Spinatum Zone, it would be the first definitely known occurrence of *Orthodactylites* below the Tenuicostatum Zone. Unfortunately Amaltheid ammonites, that would settle the date without question, are absent.

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M. K. HOWARTH, Ph.D.
Department of Palaeontology
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON SW7 5BD

PLATES

The photographs were taken by the author, and all specimens were given a thin coating of ammonium chloride.

All the figures are natural size.

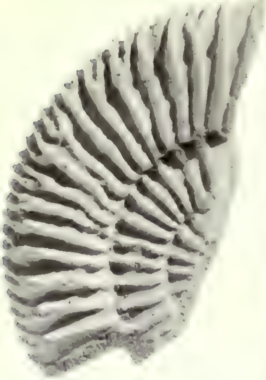
PLATE 1

Dactylioceras (Dactylioceras) pseudocommune Fucini

FIG. 1. [Top Main Dogger, lower part of Paltum Subzone], old ironstone mine, Hob Hill, near Saltburn. R. Tate collection. Institute of Geological Sciences, London, GSM 22568.

Dactylioceras (Orthodactylites) crosbeyi (Simpson)

FIGS. 2–4. Grey Shales bed 18, Clevelandicum Subzone. Fig. 2, west of Port Mulgrave, C.47950 ; Fig. 3, Holmsgrove Sand, C.76908 ; Fig. 4, Runswick Bay, C.47913.



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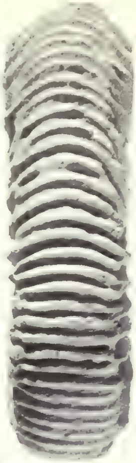

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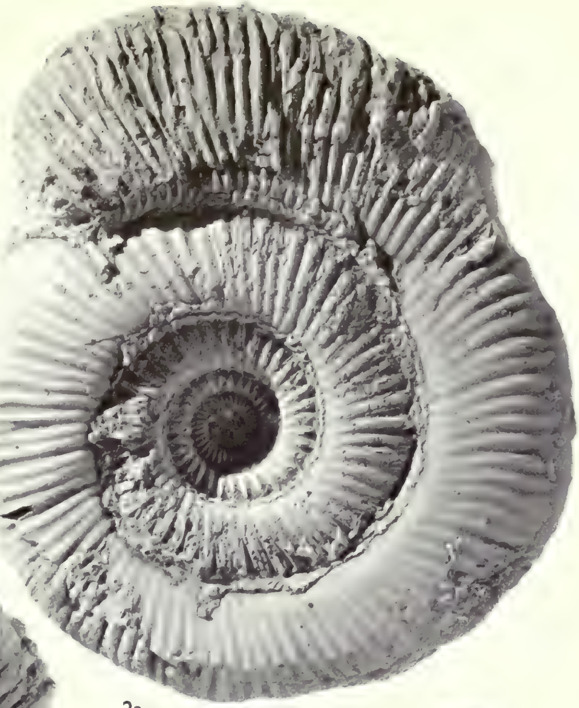

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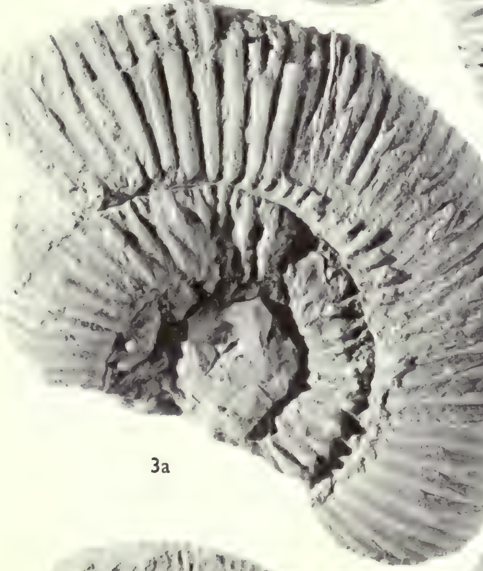

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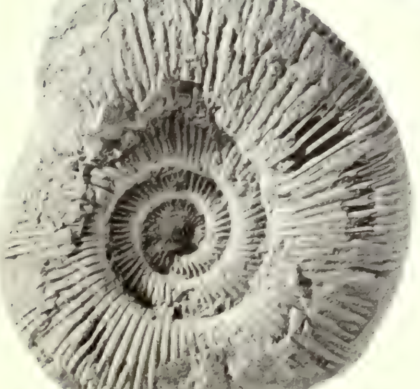

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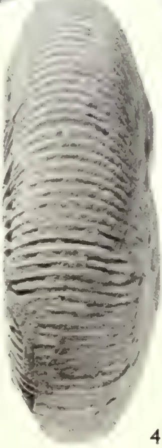

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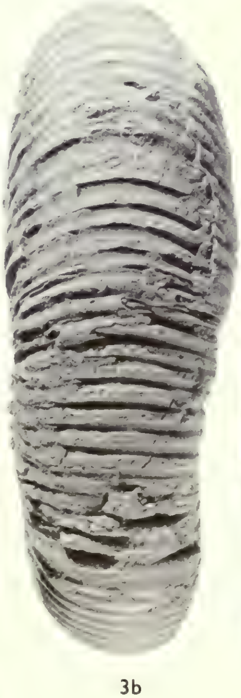

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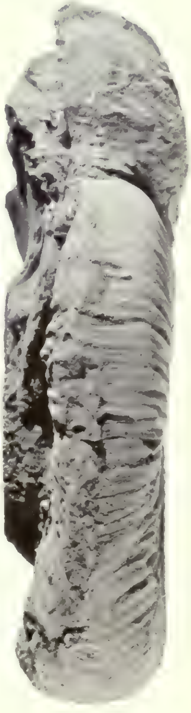

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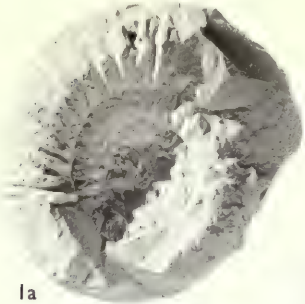
PLATE 2

Dactylioceras (Orthodactylites) crosbeyi (Simpson)
Grey Shales bed 18, Clevelandicum Subzone.

FIGS. 1, 2. East Kettleness, C.76890 and C.76886.
FIGS. 3, 4. Holmsgrove Sand, C. 76893 and C.76892.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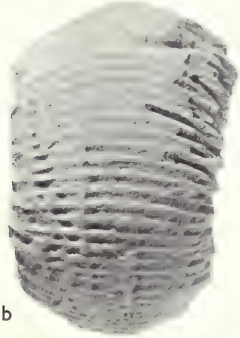
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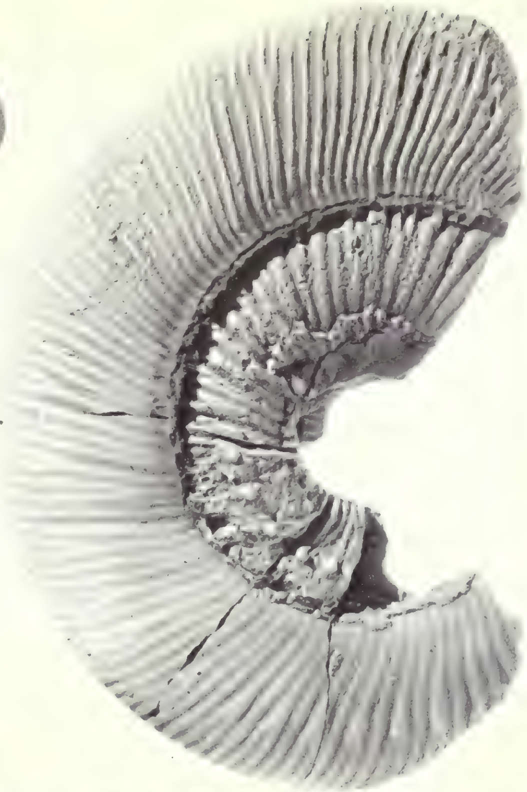
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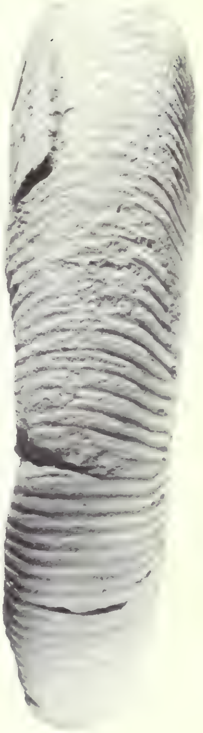
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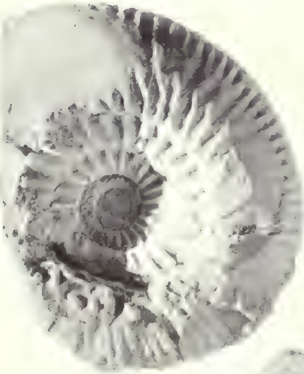
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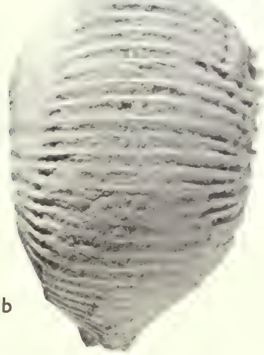
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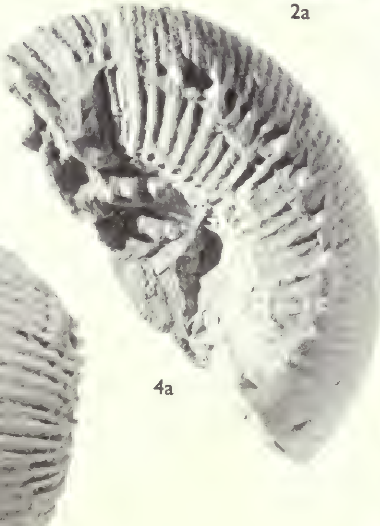
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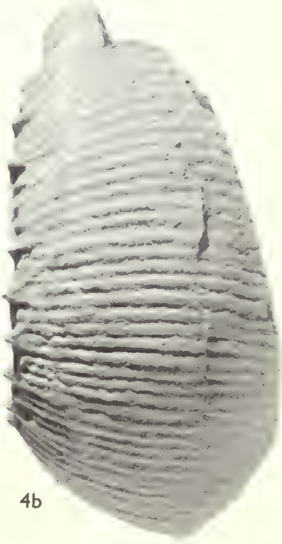
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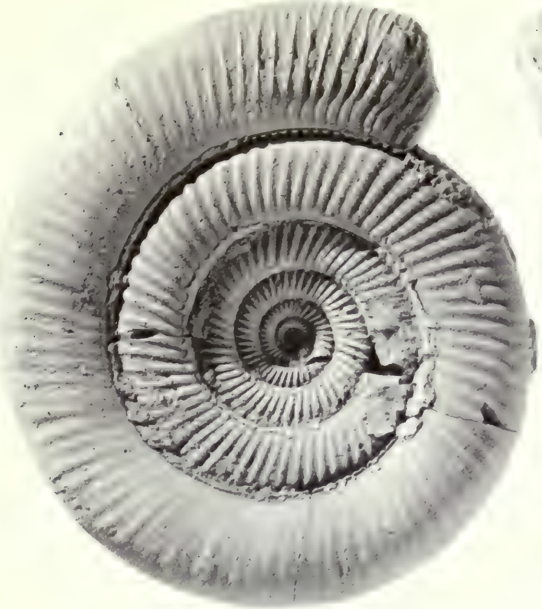
PLATE 3

Dactylioceras (Orthodactylites) clevelandicum sp. nov.

Grey Shales bed 19*b*, Clevelandicum Subzone.

FIGS. 1, 2. Holmsgrove Sand; Fig. 1. Holotype, C.77017; Fig. 2. C.76990.

FIG. 3. West of Port Mulgrave, C.76989.



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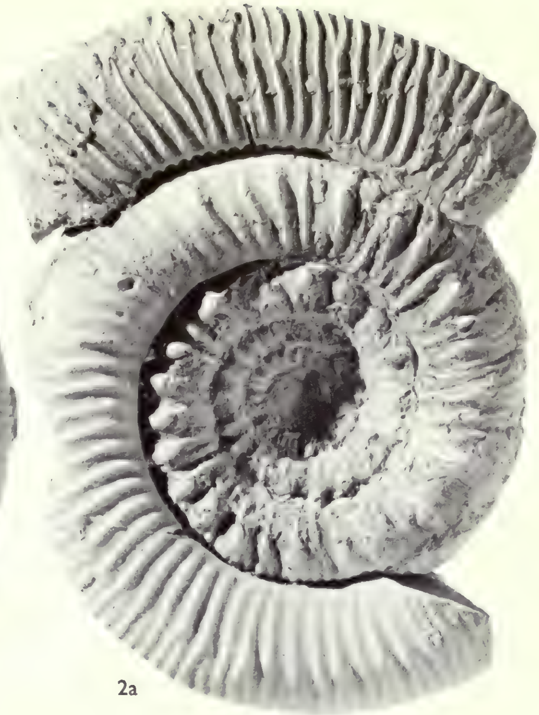

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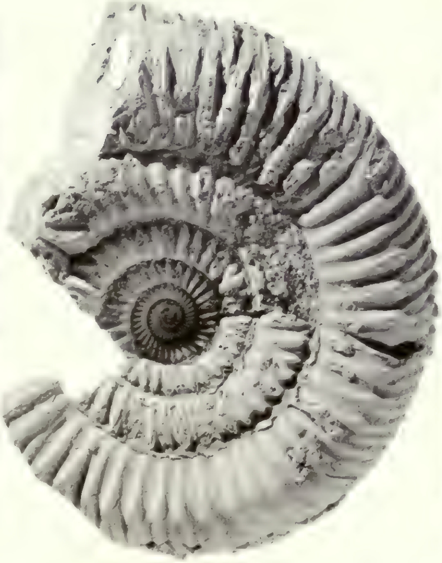

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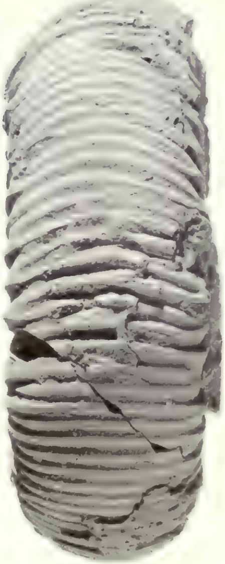

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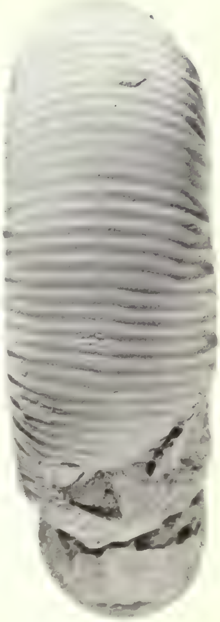

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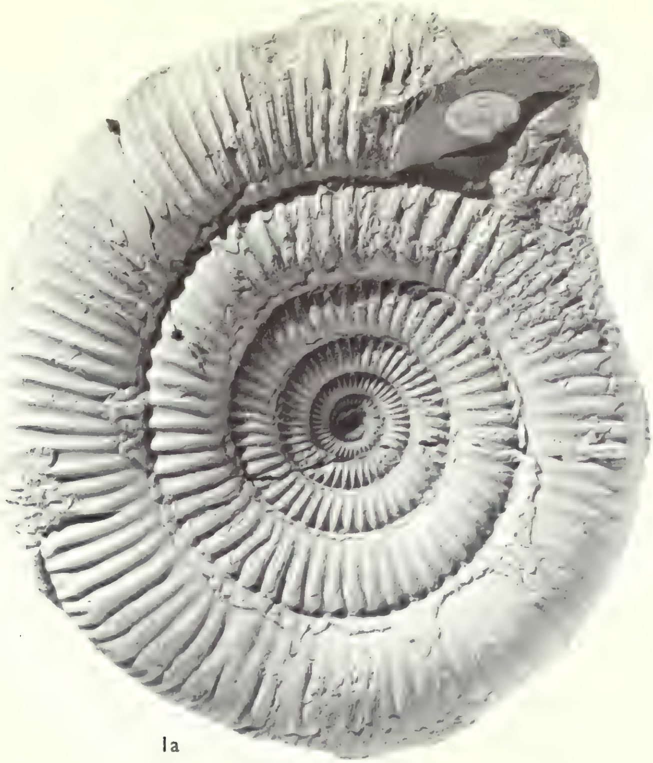
PLATE 4

Dactylioceras (Orthodactylites) clevelandicum sp. nov.

Grey Shales bed 19*b*, Clevelandicum Subzone.

FIGS. 1, 2. Holmsgrove Sand, C.76997 and C.50419.



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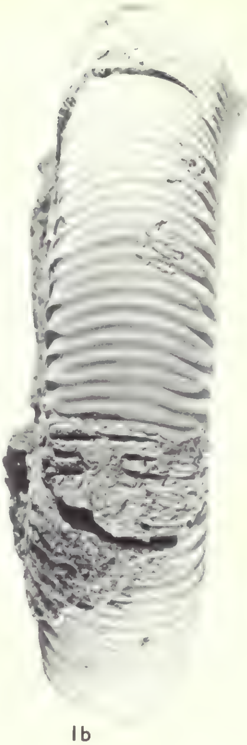

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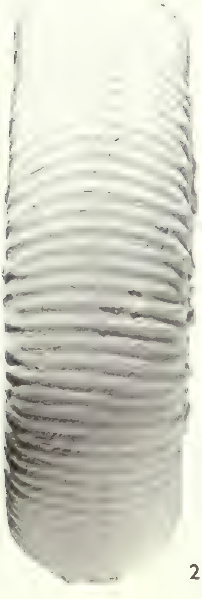

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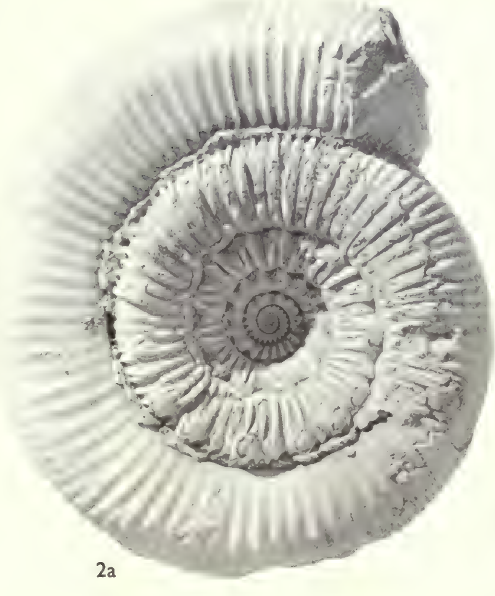

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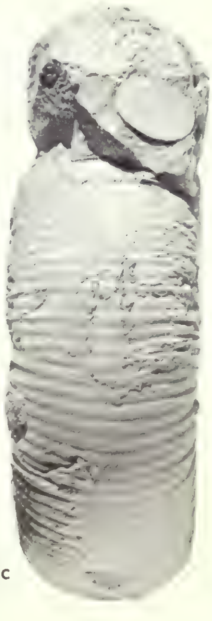

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PLATE 5

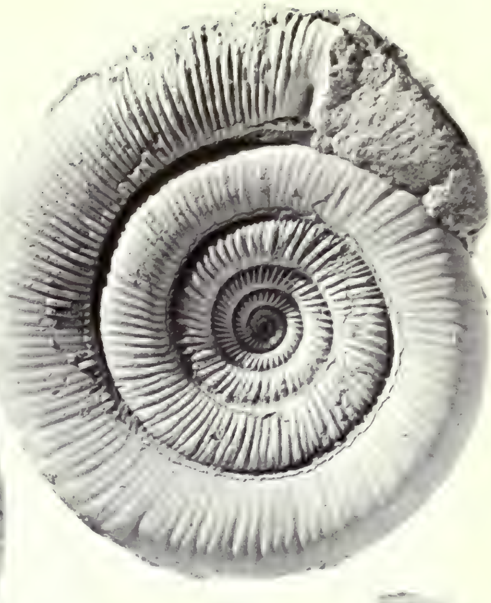
Dactylioceras (Orthodactylites) tenuicostatum (Young & Bird)

FIG. 1. Neotype, Grey Shales bed 22, Tenuicostatum Subzone, west of Port Mulgrave, C.77182.

FIG. 2. Grey Shales bed 24, Tenuicostatum Subzone, east Kettleness, C.47927.

Dactylioceras (Orthodactylites) clevelandicum sp. nov.

FIG. 3. Grey Shales bed 19*b*, Clevelandicum Subzone, east Kettleness, C.76986.



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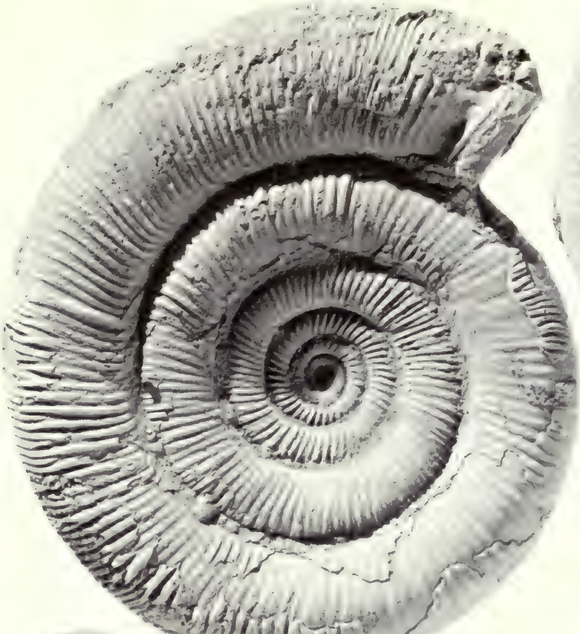

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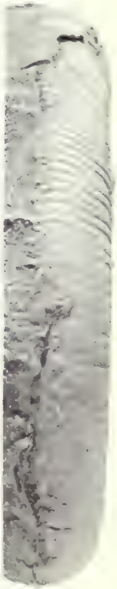

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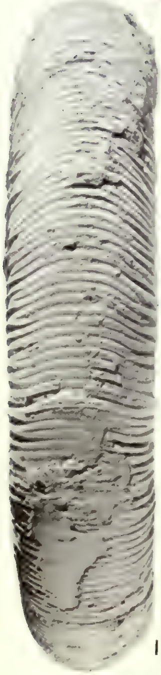

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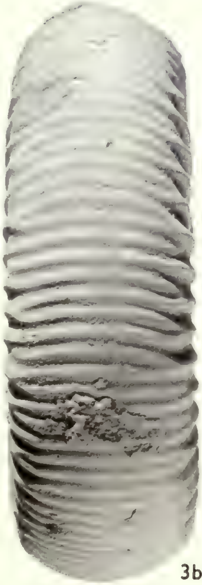

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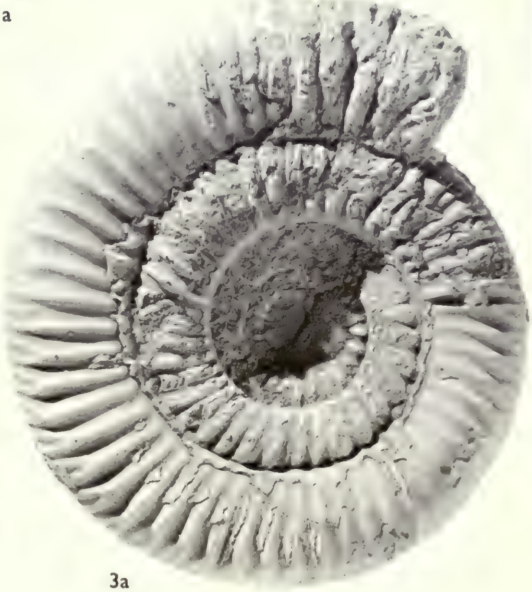

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PLATE 6

Dactylioceras (Orthodactylites) semicelatum (Simpson)

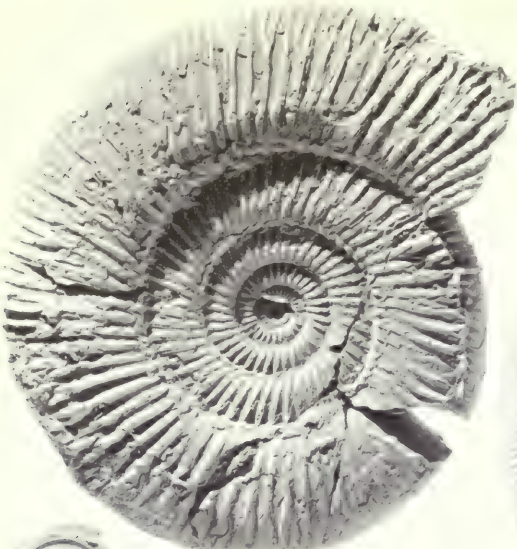
Fig. 1. Grey Shales bed 28, Semicelatum Subzone, east Kettleness, C.77270.

Dactylioceras (Orthodactylites) tenuicostatum (Young & Bird)

Tenuicostatum Subzone.

Fig. 2. Grey Shales bed 24, west of Port Mulgrave, C.77237.

Fig. 3. Grey Shales bed 20, Holmsgrove Sand, C.77109.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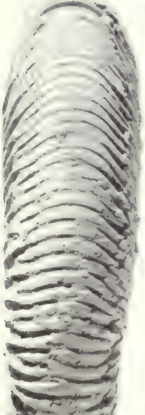
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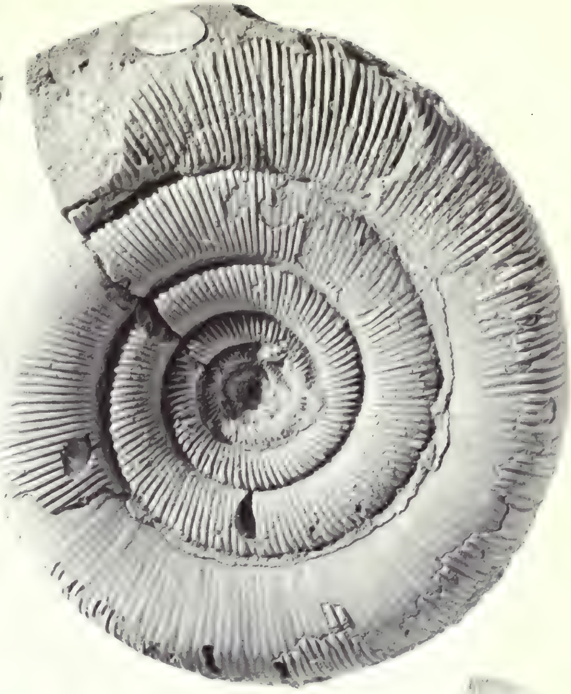
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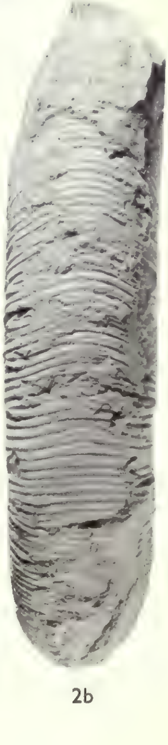
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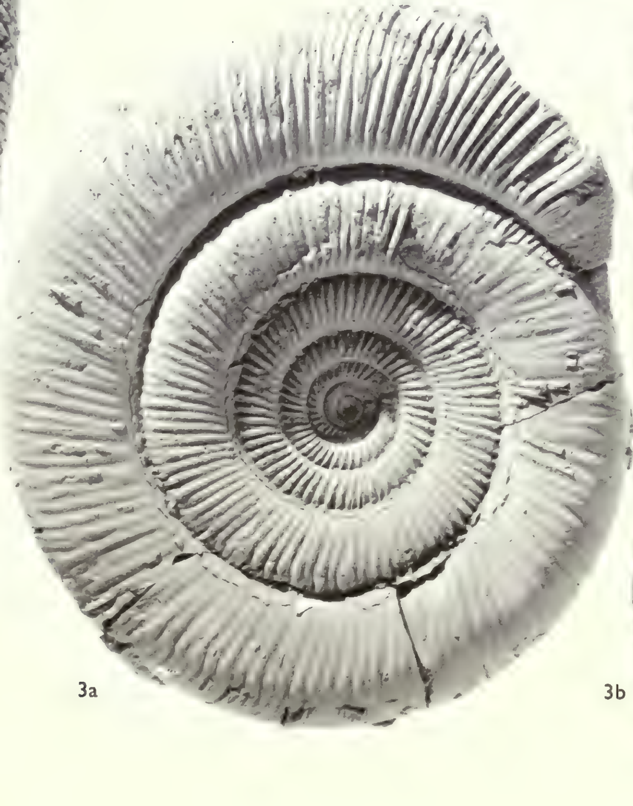
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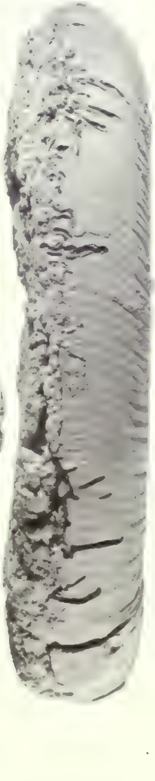
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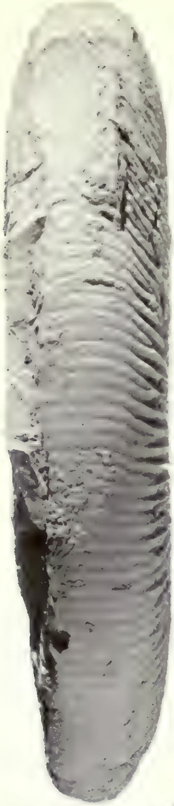
PLATE 7

Dactylioceras (Orthodactylites) semicelatum (Simpson)

Semicelatum Subzone.

FIG. 1. Grey Shales bed 30, Loop Wyke, C.77329.

FIG. 2. Grey Shales bed 28, west of Port Mulgrave, C.47940.



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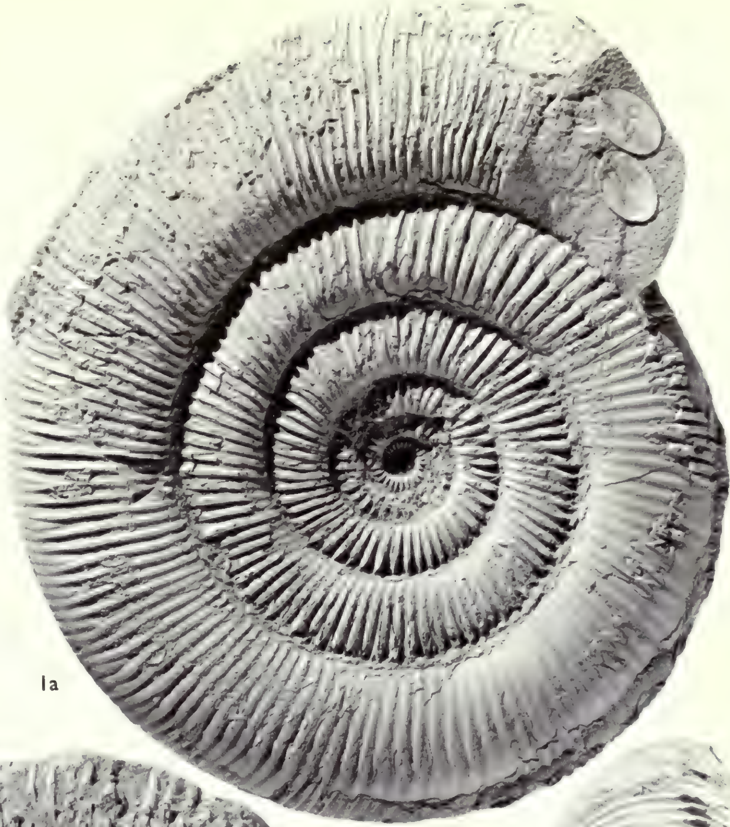

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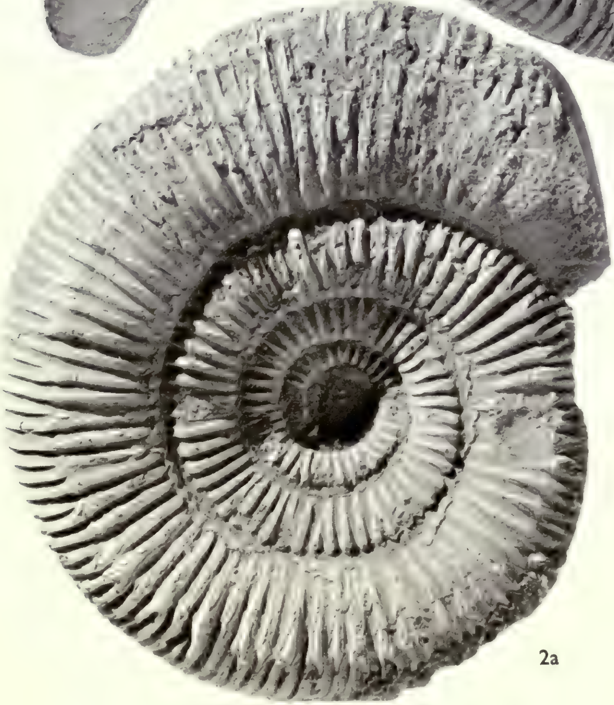

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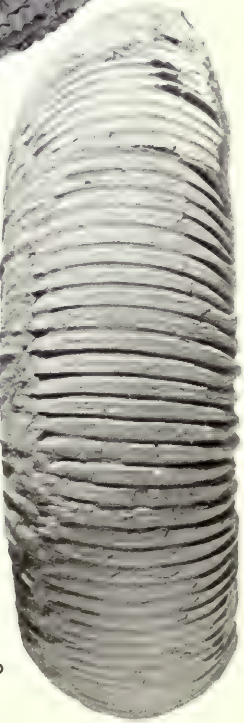

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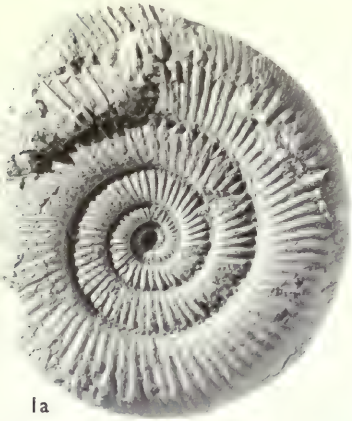
PLATE 8

Dactylioceras (Orthodactylites) semicelatum (Simpson)
Semicelatum Subzone.

FIGS. 1–3. Grey Shales bed 30, east Kettleness, C.77302, C.77305 and C.77314.

FIG. 4. Grey Shales bed 31, 1.22m (4ft) above the base, base of cliff south of Lingrow Knock, C.47932.



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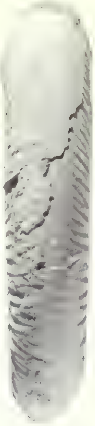

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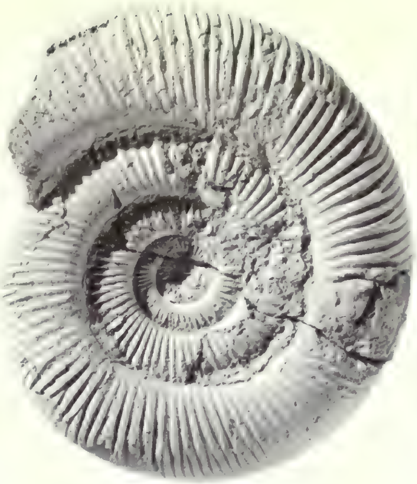

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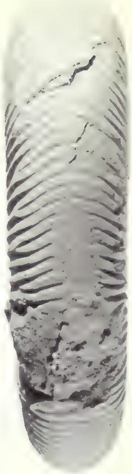

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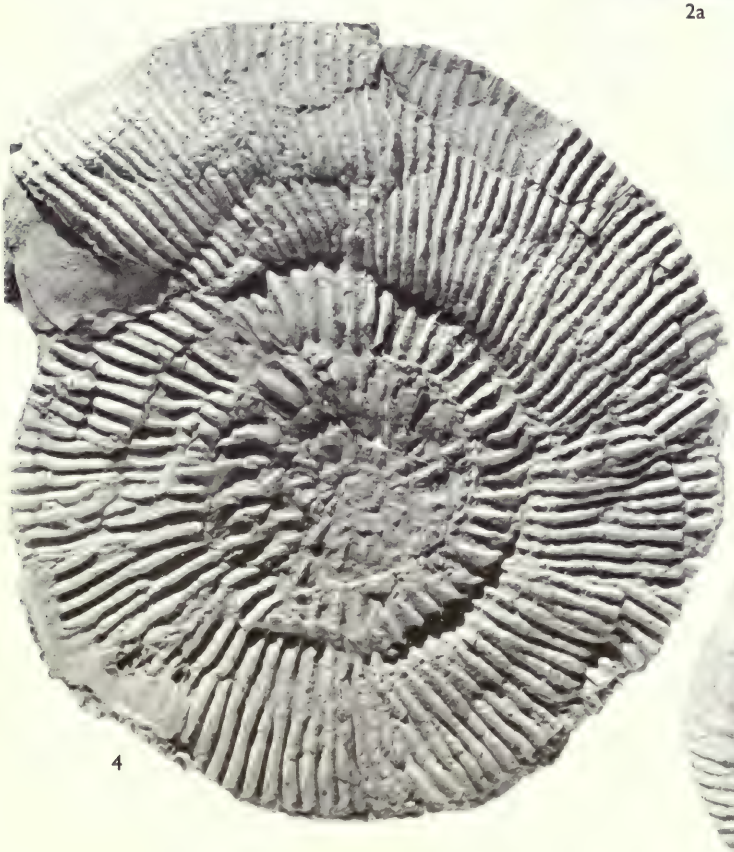

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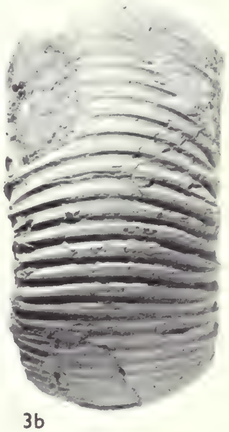

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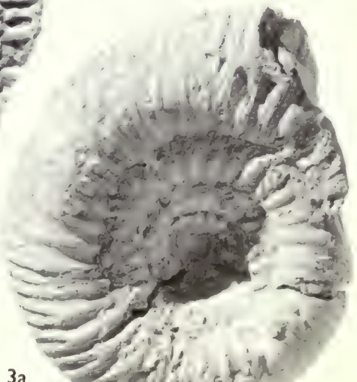


3a

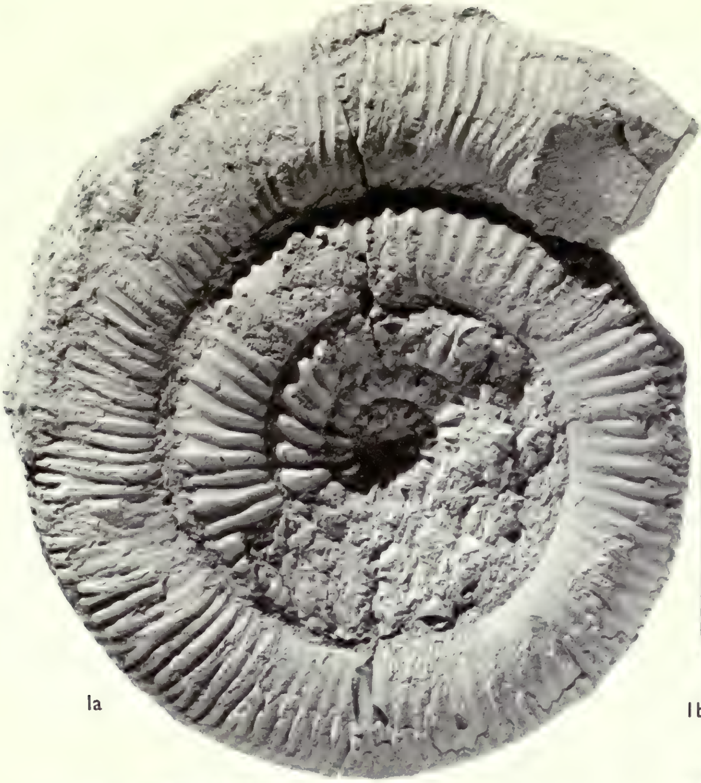
PLATE 9

Dactylioceras (Orthodactylites) semicelatum (Simpson)

Semicelatum Subzone.

FIGS. 1, 2. Grey Shales bed 30; Fig. 1. Hawsker Bottoms, C.77317; Fig. 2. West of Port Mulgrave, C.47956.

FIG. 3. With '*Posidonia*' *radiata* (Goldfuss), Grey Shales bed 32, shell bed at base, west of Port Mulgrave, C.77360.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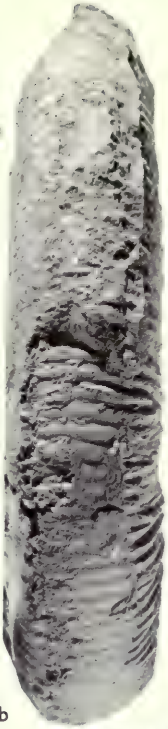
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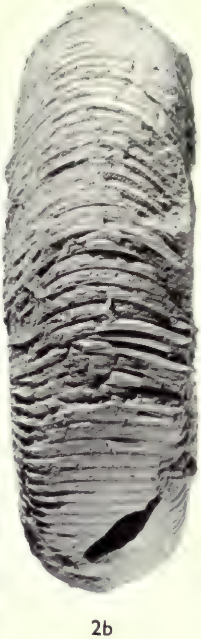
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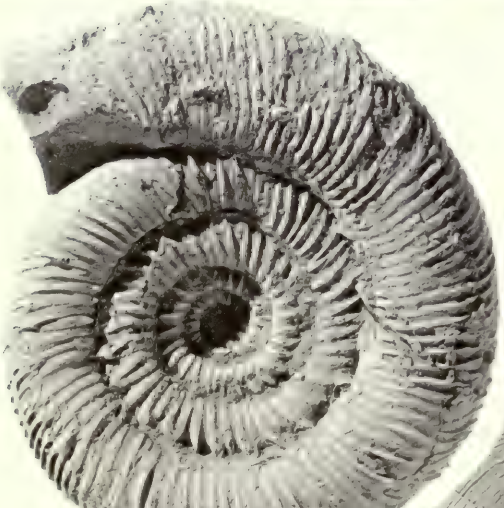
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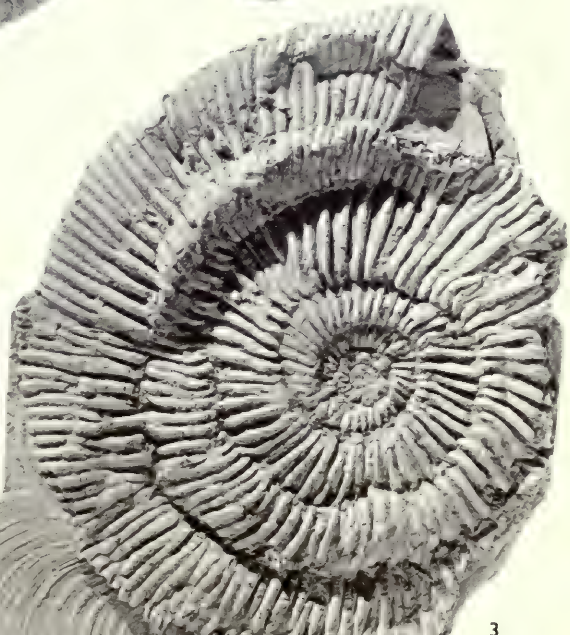
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THE LOWER PALAEOZOIC STRATIGRAPHY AND FAUNAS OF THE TAURUS MOUNTAINS NEAR BEYŞEHİR, TURKEY III. THE TRILOBITES OF THE SOBOVA FORMATION (LOWER ORDOVICIAN)

W. T. DEAN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 24 No. 5
LONDON: 1973

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THE LOWER PALAEOZOIC STRATIGRAPHY AND FAUNAS OF THE TAURUS MOUNTAINS NEAR BEYŞEHİR, TURKEY

III. THE TRILOBITES OF THE SOBOVA FORMATION (LOWER ORDOVICIAN)

BY
W. T. DEAN
Geological Survey of Canada

Pp 279–348; 12 *Plates*, 5 *Text-figures*, 2 *Tables*

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GEOLOGY Vol. 24, No. 5
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III. THE TRILOBITES OF THE SOBOVA FORMATION (LOWER ORDOVICIAN)

By W. T. DEAN

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SYNOPSIS

The strata of the Sobova Formation in the Beyşehir region form an essentially calcareous development that succeeds the Seydişehir Formation with apparent conformity. The stratigraphy of the type section in the Sobova Valley is reviewed and the trilobite fauna described. The latter includes the following new species: *Geragnostus semipolitus*, *Trinodus hebetatus*, *Agerina pamphylica*, *Phillipsinella matutina*, *Panderia monodi*, *Symphysurus pannuceus*, *Ptychopyge elegans* and *Niobe sobovana*, together with *Sobovaspis tuberculata* gen. nov., tentatively assigned to the Family Lecanopygidae. Other genera present include *Ampyx*, *Harpides*, trinucleid gen. indet., cheirurid gen. undet., *Pterygometopus* ?, *Carolinites*, *Apatokephalus*, *Pseudopetigurus*, *Metopoliches*, *Protostygina* and *Illaenus*. Many of the affinities are with Baltic faunas and the Upper Arenig age suggested by the trilobites is confirmed by associated conodonts.

Elsewhere in the area fossiliferous, pink limestones near Kızılca have been mapped as Sobova Formation. Their sparse fauna includes *Geragnostus*, *Pliomerina*, *Nileus*, *Symphysurus*, *Pricyclopyge superciliata* sp. nov. and *Euloma* (*Lateuloma*) *latigena* subgen. nov. The trilobite evidence suggests an horizon earlier than that represented by the limestones in the Sobova Valley, and associated conodonts indicate a Lower Arenig age.

I. INTRODUCTION AND ACKNOWLEDGEMENTS

THE area of the Taurus Mountains from which the present material was obtained lies some 100 km south-west of Konya and 30 km south-east of Lake Beyşehir (see Fig. 1). An account of the stratigraphy of the Cambrian and Ordovician rocks in the Beyşehir–Seydişehir region was given in an earlier publication (Dean & Monod 1970). A subsequent paper (Dean 1971) described the trilobites, all of Lower Arenig age, in the higher, fossiliferous portion of the Seydişehir Formation, and the present work deals with the trilobites of the overlying Sobova Formation.

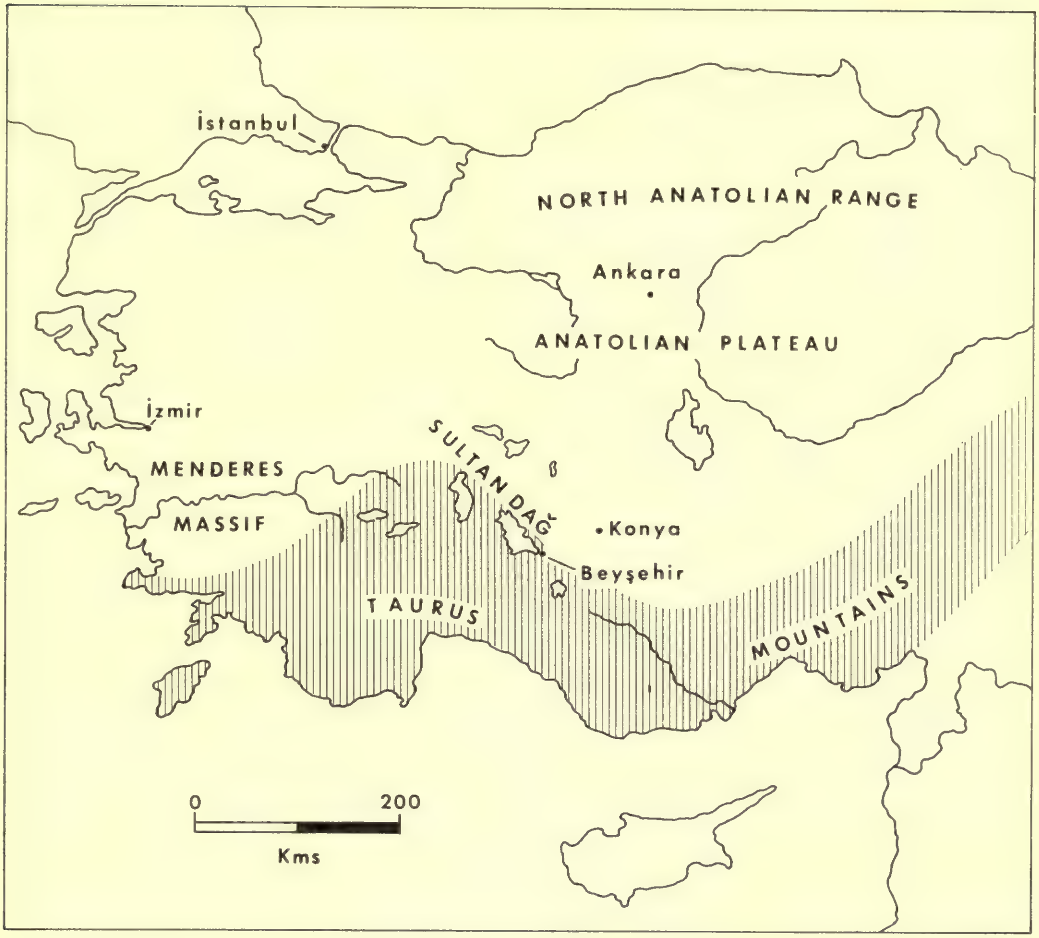
İstanbul
NORTH ANATOLIAN RANGE
Ankara
ANATOLIAN PLATEAU
İzmir
MENDERES
MASSIF
SULTAN DAĞ
Konya
Beyşehir
TAURUS
MOUNTAINS
0
200
Kms

FIG. 1. Sketch-map of western Turkey, showing the location of the Beyşehir region in the Taurus Mountains.

Ordovician rocks form extensive outcrops in the region (see Fig. 2, a generalized geological map based on the work of Monod, *in* Dean & Monod 1970) but most are shales, siltstones and quartzites, usually unfossiliferous, belonging to the Seydişehir Formation. The strata of the Sobova Formation represent a marked change of lithology and the lower portion, the Sobova Limestone member, is particularly noticeable. Outcrops of the formation are relatively small and widely scattered, having been found at only three places: (i) the Sobova Valley, 22 km north-west of Seydişehir (fossil locality B.651); (ii) in the vicinity of Kızılca, both 1·75 km east (locality C.429) and 0·75 km west (locality C.432) of the village; (iii) 1 km north-west of the village of Taraşçı, about 7 km west-northwest of

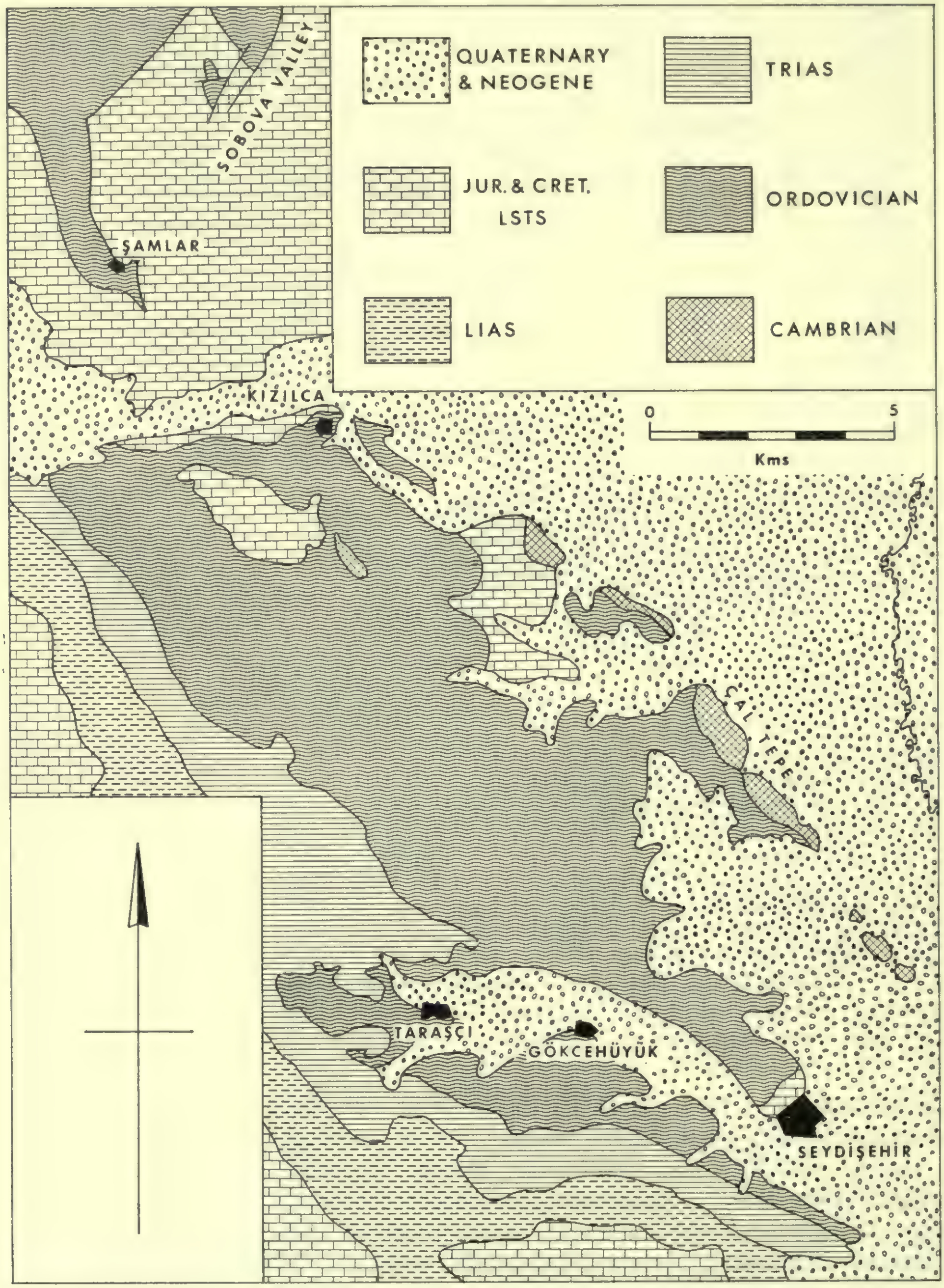
QUATERNARY & NEOGENE
TRIAS
JUR. & CRET. LSTS
ORDOVICIAN
LIAS
CAMBRIAN
0
5
Kms
SOBOVA VALLEY
ŞAMLAR
KIZILCA
ÇAL TEPE
TARAŞÇI
GÖKCEHÜYÜK
SEYDİŞEHİR

FIG. 2. Map to show the position of the Sobova Valley and village of Kızılca in relation to Seydişehir, 30 km south-southeast of Beyşehir. Generalized geological boundaries after Monod (*in* Dean & Monod 1970).

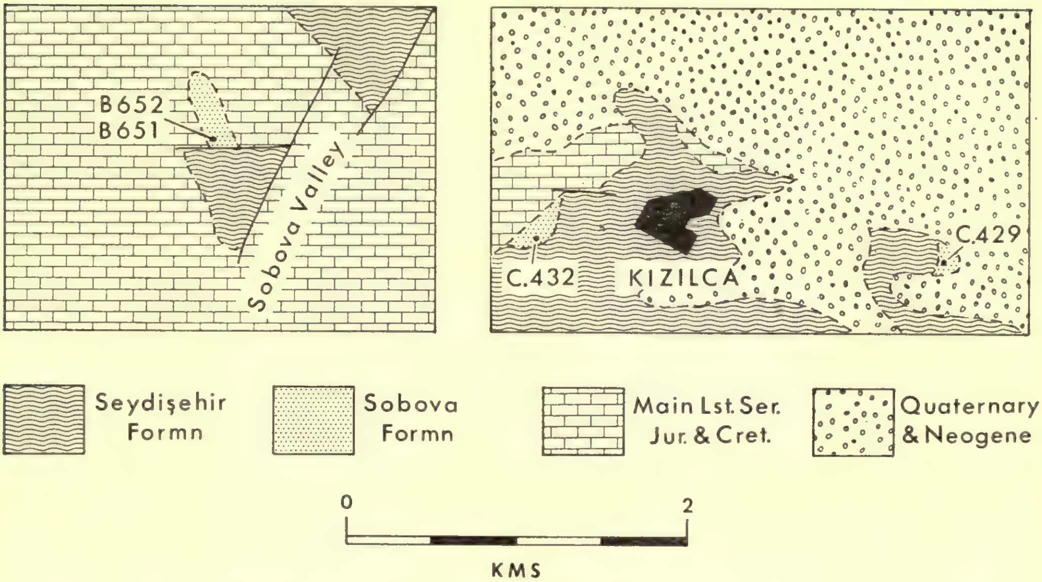

FIG. 3. Fossil localities in the Sobova Limestone member of the Sobova Formation at the Sobova Valley and near Kızılca.

Seydişehir, where locality C.217 yielded only unrecognizable traces of fossils. The rocks exhibit marked changes of lithology when traced laterally, and detailed correlation is difficult in the absence of complete sections.

At its type section in the Sobova Valley, the Sobova Formation overlies the Seydişehir Formation with apparent conformity, though the actual line of contact is obscured and may, in fact, be a disconformity in view of the age relationships indicated by the trilobite faunas (see p. 339 and Fig. 5). The section is located on the north-western side of the Sobova Valley (see Figs. 2, 3) where the Sobova Limestone member consists of about 10 metres of tough, partially crystalline, pink and grey limestone, containing fossils at loc. B.651, mostly trilobites which may be locally abundant, though fragmentary and sometimes distorted. These strata are overlain by almost 20 metres of grey shales, unfossiliferous except for a thin bed of limestone at the base of the highest third.

The southernmost outcrop of the Sobova Formation is north-west of Taraşçı. There the basal limestone member has diminished in thickness to only 2 metres, and is succeeded by an estimated 18 metres of red sandstones that are presumed to be the lateral equivalents of the higher, shaly member in the Sobova Valley. The Sobova Formation near Taraşçı is overlain unconformably by the Taraşçı Limestone, of Triassic age, but the junction is obscured and the highest Ordovician strata were not available for collecting.

The outcrops of Sobova Formation in the vicinity of Kızılca, although intermediate geographically between those of the Sobova Valley and Taraşçı, nevertheless exhibit marked differences from both, and their stratigraphical relationships are

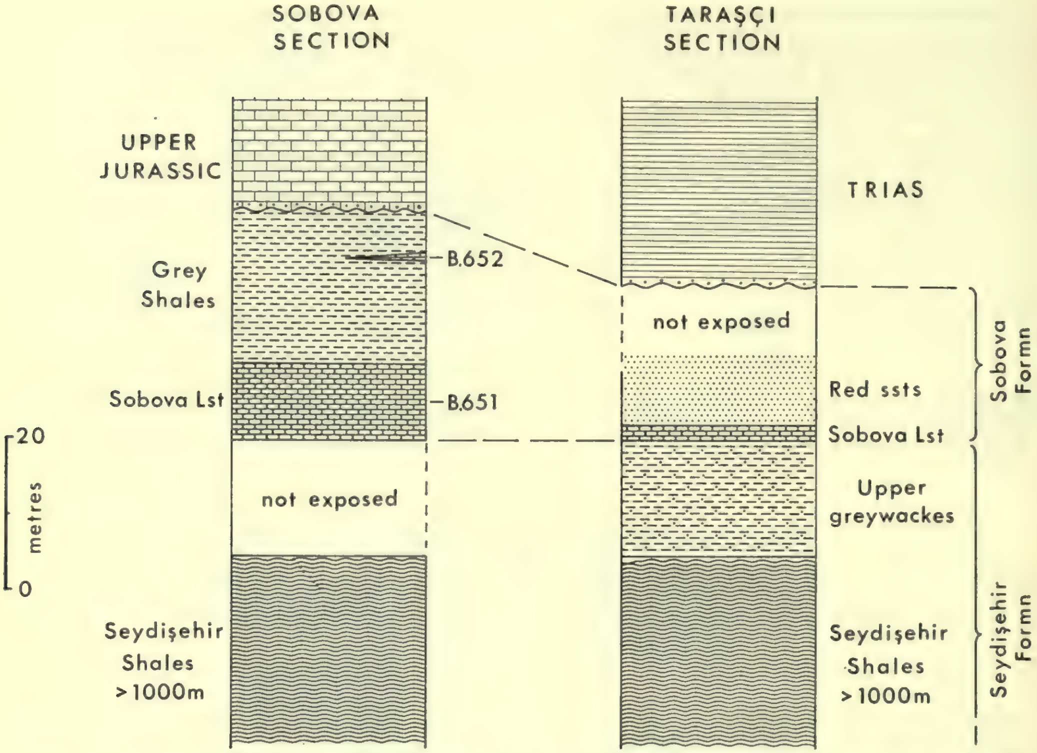
SOBOVA SECTION
TARAŞÇI SECTION
UPPER JURASSIC
Grey Shales
B.652
Sobova Lst
B.651
20
metres
0
not exposed
Seydişehir Shales >1000m
TRIAS
not exposed
Red ssts
Sobova Lst
Upper greywackes
Seydişehir Shales >1000m
Sobova Formn
Seydişehir Formn

FIG. 4. Stratigraphical position of the fossil localities in the limestone member of the Sobova Formation and the relationships of the strata to corresponding beds near Taraşçı. The sequence of strata near Kızılca is not known with certainty.

not yet clear. At localities C.429 and C.432 there occurs a white and grey limestone, often saccharoidal in appearance with many patches of crystalline calcite. Not only is it lithologically distinct from the lower, limestone member of the Sobova Valley, but the fauna, again essentially trilobitic, is different. The difference in fauna is thought to be due to a slight discrepancy in age rather than the result of lateral changes in lithology, and the subject is discussed in detail later in this paper.

The material for the present paper was obtained in company with M. Olivier Monod, to whom I am grateful for his ready help and collaboration while collecting in the Beyşehir region. Professor H. B. Whittington, as on several previous occasions, kindly read the manuscript critically, and I am particularly indebted to Dr Valdar Jaanusson who gave me the benefit of his own researches on Ordovician faunas of the Baltic region.

II. SYSTEMATIC DESCRIPTIONS

The terminology employed in the following pages is essentially that advocated in the *Treatise on Invertebrate Paleontology* (Harrington, Moore & Stubblefield *in* Moore 1959 : O 117), though some of the terms were described by them as being less important. For agnostids Whittington (1963 : 28) has been followed. The brief trinucleid description uses the terms recommended by Whittard (1955 : 27) and based partly on earlier work by Reed and Bancroft, whilst the use of ' arc ' for concentric rows of fringe-pits is due to Hughes (1970). The trilobite remains are almost all fragmentary, only a single complete exoskeleton (of *Symphysurus pannuceus* sp. nov.) having been collected. Consequently there has been some difficulty in assigning less obvious fragments to the correct genus, and this is particularly the case for immature or broken asaphid remains.

Family **AGNOSTIDAE** M'Coy, 1849

Genus ***GERAGNOSTUS*** Howell, 1935

TYPE SPECIES. *Agnostus sidenbladhi* Linnarsson, 1869.

Geragnostus semipolitus sp. nov.

(Pl. 1, figs. 2, 4, 5, 7–12, 14, 16, 17)

DIAGNOSIS. Species of *Geragnostus* distinguished especially by pygidium, axis of which is relatively short for genus, just over half total length of pygidium. Outline well rounded with broad border. Anterior two-fifths of axis well defined with two axial rings, and median longitudinal segment produced to form short spine ; posterior three-fifths of axis poorly defined, even on internal mould and less so on external surface, with median tubercle near narrow rounded tip.

HOLOTYPE. BM. It.7887 (Pl. 1, figs. 4, 5, 11).

PARATYPES. BM. It.7886 (Pl. 1, fig. 2), It.7888 (Pl. 1, fig. 9), It.7889 (Pl. 1, fig. 12), It.7893 (Pl. 1, fig. 8), It.7894 (Pl. 1, fig. 10), It.7895 (Pl. 1, figs. 7, 14, 16), It.7896 (Pl. 1, fig. 17).

LOCALITY AND HORIZON. Locality B.651 at the Sobova Valley, south of Beyşehir, in the Sobova Limestone member of the Sobova Formation.

DESCRIPTION. The cranidium is subsemicircular in outline and generally resembles that of the type and other species of *Geragnostus*. The glabella occupies two-thirds to three-quarters of the median length and tapers gently forwards to a well-rounded anterior lobe. The hindmost portion of the glabella is plump, obtusely pointed, and flanked by a pair of subtriangular lateral lobes of the occipital ring that are in turn joined by a small median band. The sides of the glabella have a pair of small indentations opposite the centre, just in front of which is a small, slightly elongated median tubercle. The border is broadest (*sag.*) frontally, equal to one-twelfth of the overall cranidial length, but narrows posterolaterally.

The pygidium is almost semicircular in outline with the breadth increasing slightly from the anterior margin to attain its maximum opposite the mid-point. The axis is sub-triangular, occupying about half the anterior breadth of the pygidium and extending backwards for slightly more than half the median length ; the sides are almost straight and converge backwards at about 32 degrees to the small, semi-elliptical tip. The anterior portion, a little less than half, of the axis consists of two subequal axial rings, both of them traversed medially by a longitudinal segment, the posterior part of which is produced upwards and slightly back to form a blunt spine; the axial rings are separated by ring furrows which are broadly divergent posteriorly. All the furrows of the anterior part of the axis appear deep on the internal mould and, although shallower on the outer surface of the exoskeleton, nevertheless are easily discernible. The axial furrows delimiting the posterior part of the axis are much less marked on the internal mould and, together with the median tubercle near the tip of the axis, may appear almost effaced on the outer surface (compare Pl. 1, figs. 5, 12, internal moulds, with Pl. 1, figs. 2, 9, showing the outer surface). The border is notably broad, especially posteriorly where it occupies nearly one-quarter of the pygidial length, but narrows anterolaterally.

Dimensions (in mm, IM = internal mould, EM = external mould).

	It. 7886	It. 7887	It. 7888	It. 7889	It. 7893	It. 7894	It. 7895	It. 7896
Length of cranidium	–	–	–	–	–	–	–	2·4 (EM)
Max. breadth of cranidium	–	–	–	–	–	–	3·2 (IM)	2·2 (EM)
Length of glabella	–	–	–	–	2·0 (EM)	2·1 (IM)	1·8 (IM)	1·4 (EM)
Max. breadth of glabella	–	–	–	–	1·2 (IM)	1·3 (IM)	1·2 (IM)	0·9 (EM)
Length of pygidium	4·0 (IM)	3·1 (IM)	3·5 (EM)	3·1 (EM)	–	–	–	–
Max. breadth of pygidium	4·0 (IM)	3·2 (IM)	3·8 (EM)	3·2 (EM)	–	–	–	–
Frontal breadth of axis	2·0 (IM)	1·4 (IM)	1·7 (EM)	1·4 (EM)	–	–	–	–

Discussion. The form of the pygidial axis of *G. semipolitus* is closely comparable with that of *G. tullbergi* (Novák), the type species of *Geragnostella*, a genus sometimes regarded as a synonym of *Geragnostus* (Dean 1966 : 273). The two species have in common a fairly strongly convergent axis in which the posterior half or more is scarcely defined, though the anterior portion has strong axial furrows and two well-defined axial rings with a conspicuous, longitudinal, blunt spine. *G. tullbergi* is from the Šárka Beds, Llanvirn Series, of Bohemia and is thus slightly younger than the new species. *Geragnostus occitanus* Howell (1935 : 231 ; see also Dean, 1966 : 274), from the Lower Arenig of southern France, also has a median tubercle on the pygidial axis, but it is not sited so far back as in *G. semipolitus*. *Geragnostus lycaonicus* Dean (1971 : 6, pl. 1, figs. 3, 5, 8), from the Seydişehir Formation of the Sobova Valley, has a pygidium generally similar to that of the new species but may be distinguished by its longer, broader axis and by the different form of the axial ring furrows, which are curved, concave forwards. The pygidium of *Geragnostus* ? *explanatus* Tjernvik (1956 : 193, pl. 1, figs. 13, 14), from the 'Grey Lower Planilimbata Limestone' of Sweden, also has the abaxial portions of the ring furrows strongly curved and concave forwards, particularly in the case of the first axial ring, the outer thirds of which form a pair of discrete lateral lobes, at least on the internal mould.

Geragnostus sp.

(Pl. 1, figs. 1, 3)

Figured specimens. BM. It.7891 (Pl. 1, fig. 1) ; It.7892 (Pl. 1, fig. 3).

Locality and horizon. Locality C.429, 1·5 km east of Kızılca, in limestones of the Sobova Formation.

Description. *Geragnostus* is rare at this locality and only two specimens have so far been found. The cranidium is incomplete but expands forwards for two-thirds of its length to attain a maximum breadth which is slightly greater than the median length. The outline is well rounded, with a narrow border ; the axis occupies two-thirds of the median length but only one-third of the maximum breadth, and is semielliptical in outline with gently converging sides. There is a small tubercle positioned just behind centre, and a pair of small basal lobes. The pygidium is only slightly longer than broad, and the relatively large axis occupies two-thirds of the length and half the breadth. The axial outline is only gently convergent for most of its length, with a well-rounded tip, but the frontal portion, comprising two axial rings, tapers backwards slightly. The species does not compare closely with any previously described form and is certainly distinct from the species found at locality B.651, but the material is inadequate for erecting a new specific name.

Dimensions. (IM = internal mould, EM = external mould.) Length of cranidium = 1·9 mm estd (IM), max. breadth of cranidium = 1·8 mm estd (IM), length of glabella = 1·0 mm (IM), max. breadth of glabella = 0·7 mm (IM), length of pygidium = 1·5 mm estd (IM), breadth of pygidium = 1·5 mm estd (IM), length of axis = 1·0 mm (IM), max. breadth of axis = 0·8 mm (IM).

Genus ***TRINODUS*** M'Coy, 1846

Type species. *Trinodus agnostiformis* M'Coy, 1846.

Trinodus hebetatus sp. nov.

(Pl. 1, figs. 6, 13, 15)

Diagnosis. Pygidium slightly broader than long, with well-developed border that is broadest posterolaterally. Axis less than half pygidial length, with truncated tip ; two unequal axial rings occupy anterior three-fifths of axis, their median third forming longitudinal tubercle.

Holotype. BM. It.7890.

Locality and horizon. B.651 at the Sobova Valley, in the limestone member of the Sobova Formation.

Description. A single distinctive pygidium has the outline subquadrate, broadly rounded posteriorly and is strongly convex both longitudinally and transversely, a little broader than long. The axis is particularly conspicuous, having a length just less than half that of the pygidium, and trapezoidal in plan with almost straight sides converging at about 32 degrees to a broad, truncated tip that is bounded by a deeper, broader (*sag.*) continuation of the axial furrows. The pleural regions are circumscribed by a broad lateral border furrow, followed in turn by a border that is broadest posterolaterally and narrows anterolaterally, where a pair of facets is developed. The axis is divided into two unequal parts, the anterior of which occupies three-fifths of the axial length and is in turn subdivided into two unequal axial rings, the anterior of which is the smaller and forms a pair of lateral lobes. Almost the median third of the combined first and second axial rings is occupied by a parallel-sided longitudinal ridge that thickens posteriorly to form a tubercle-like structure. On either side of this ridge the first ring furrow runs slightly backwards abaxially, but immediately behind it the second ring furrow is transversely straight. The sides of the axis are not quite straight and there is a suggestion of a break in outline, abaxially concave, opposite the centre of the second axial ring.

DIMENSIONS. (IM = internal mould.) Length of pygidium = 2·5 mm (IM), max. breadth of pygidium = 3·1 mm (IM), length of axis = 1·2 mm (IM), frontal breadth of axis = 1·3 mm (IM).

DISCUSSION. Although one can be reasonably confident of identifying an example of *Geragnostus* or *Trinodus* that agrees in most respects with the type species of either genus, some species may be more difficult to place and the Turkish specimen is a case in point. The pygidial axis, which occupies just less than half the pygidial length (excluding articulating half-ring) is slightly longer than that of a typical *Trinodus* such as *T. tardus* (Barrande) (see Whittington 1950 : pl. 68, figs. 4–6 ; 1968 : 97), but far from as long as that of the type *Geragnostus*, *G. sidenbladhi* (Linnarsson) (see Tjernvik 1956 : 188). The truncated axial tip is closer to that of *Trinodus* and I prefer to place the specimen in that genus. A somewhat similar problem is that of a pygidium from the Arenig Series of Bornholm listed originally by C. Poulsen (1936 : 49) as *Trinodus* but described later by V. Poulsen (1965 : 61, pl. 1, figs. 1–3) as *Geragnostus danicus*. The pygidial axis of *G. danicus* is almost half the pygidial length and has straight sides and a truncated tip. According to V. Poulsen (*loc. cit.*), in *Geragnostus* the axis should be tapered as far as the second axial ring furrow and then parallel-sided, but this is clearly an exaggeration judging from Tjernvik's illustrations of the type species. Ross (1967 : D8, 9) has reinterpreted certain species placed originally in *Geragnostus* by Whittington (1963 : 28) and assigned them to *Trinodus*, but Whittington (1968 : 97) has since reaffirmed their inclusion in *Geragnostus* and his reasoning is followed here. Comparable difficulties were experienced by Harrington & Leanza (1957 : 73, 74) when describing *Trinodus* ? *saltaensis* from the Upper Tremadoc of Argentina. This species has a pygidial axis unusually long for the genus, slightly longer even than in the Turkish form, and differs also from the latter in being slightly broader overall and having less straight ring furrows.

In certain respects the pygidium of *T. hebetatus* resembles that of *Galbagnostus galba* (Billings), described originally from the middle Table Head Formation of Newfoundland and since redescribed by Whittington (1965 : 305). Both species have a similar outline and a straight-sided axis with blunt tip. The axis of *G. galba* is, however, the more strongly tapered and the median portion of the third axial ring protrudes backwards towards a low tubercle sited centrally, just behind the axial furrow. The exoskeleton of *G. galba* is conspicuously ornamented with a mesh-like pattern of low ridges, but that of *T. hebetatus* shows only a suggestion of ornamentation, even under high magnification.

Family **RAPHIOPHORIDAE** Angelin, 1854

Genus ***AMPYX*** Dalman, 1827

Type species. *Ampyx nasutus* Dalman, 1827.

Ampyx sp.

(Pl. 2, figs. 1, 4, 7, 11)

Figured specimen. BM. It. 7897.

Locality and horizon. B.651 at the Sobova Valley section, in the Sobova Limestone member of the Sobova Formation.

Description. A single cranidium preserved as an internal mould which lacks the frontal spine has a basal breadth just over twice the median length of the glabella. The glabella is defined basally by a broad (*sag.*), shallow occipital furrow from which it expands forwards so as to attain its maximum breadth, equal to approximately two-thirds of the median length, opposite the centre and then narrows again more rapidly to the base of the frontal spine. The large frontal lobe so formed projects beyond the fixigenae and is triangular in plan but almost conical in form, its cross-section sub-circular. The axial furrows are broad and well defined, diverging forwards at about 45 degrees until opposite the mid-point of the glabella, where they become narrower and deeper, and curve down and inwards so as to circumscribe the front of the glabella and meet frontally (see Pl. 2, fig. 7).

Dimensions. (IM = internal mould.) Median length of cranidium (to base of frontal spine) = 5·0 mm estd (IM), basal breadth of cranidium = 8·8 mm estd (IM), max. breadth of glabella = 2·8 mm (IM).

Discussion. The type species, *Ampyx nasutus* Dalman from the Expansus or lower Raniceps Limestone of uppermost Arenig or lowest Llanvirn age in Östergötland, Sweden, was redescribed by Whittington (1950 : 554, pl. 74, figs. 3–9). His illustrations show that the present form differs in having the axial furrows more divergent forwards whilst the frontal glabellar lobe is longer and more pointed. The abaxial ends of the posterior border furrow contain a pair of pits similar to those illustrated by Whittington (1950 : text-fig. 6A), but the glabella exhibits neither anterior pits nor pairs of muscle-scars like those of *A. nasutus*, though the absence of the latter structures was noted also in *Ampyx compactus* Ross (1967 : D 21) from the Antelope Valley Limestone of California, a species of which the frontal glabellar lobe is slightly shorter and less pointed than that of the Sobova specimen.

Family **HARPIDIDAE** Whittington, 1950

Genus ***HARPIDES*** Beyrich, 1846

TYPE SPECIES. *Harpides hospes* Beyrich 1846.

Harpides sp.

(Pl. 2, figs. 10, 12)

FIGURED SPECIMENS. BM. It.7903 (Pl. 2, fig. 10), It.7904 (Pl. 2, fig. 12).

LOCALITY AND HORIZON. B.651 at the Sobova Valley, in the limestone member of the Sobova Formation.

DESCRIPTION. The better-preserved (Pl. 2, fig. 12) of the two available fragments of harpidid cephalic fringe at this locality shows part of the ventral lamella with its characteristic girders running parallel to the cephalic margin. The concave concentric bands between the girders are traversed by radiating ridges (see Pl. 2, fig.12) which correspond in position to genal caeca on the dorsal lamella. These radial ridges do not cross the girders and they are separated from each other by radial sulci that contain several, generally 9 to 13, small pits. The dorsal lamella of the same fringe fragment bears a radial pattern of low broad, low, poorly-defined ridges – the genal caeca – separated by shallow sulci of approximately similar size. The caeca are covered with granules whilst the sulci contain numerous small pits, some of which exhibit a rudimentary paired arrangement. Both this specimen and another, a fragment of external mould (Pl. 2, fig. 10) show a suggestion of scarcely discernible concentric ridges on the dorsal lamella, set lower than the radial ridges and corresponding in position approximately to the concentric girders on the ventral lamella.

DISCUSSION. *Harpides* ranges from Tremadoc Series to approximately lower Llanvirn Series, and the best-known species, *H. atlanticus* Billings, 1865 from the Table Head Formation of western Newfoundland (see Whittington, 1965 : 309, pls. 5–7) is also the youngest. In spite of the fragmentary nature of the Sobova material it can be seen to resemble *H. atlanticus* in some respects, particularly the form of the ventral girders, though the distance from the margin to the outermost girder is relatively smaller, whilst the radiating sulci between the caeca on the ventral lamella are deeper. In addition the dorsal lamella does not have the pronounced smooth concentric bands described by Whittington as corresponding to the ventral girders, but, as noted above, there are poorly defined concentric ridges in analogous positions, set slightly lower than the radial caeca and ornamented with granules.

Harpidid gen. et sp. indet.

(Pl. 2, fig. 9)

FIGURED SPECIMEN. BM. It.7902.

LOCALITY AND HORIZON. C.429, 1·5 km east of Kızılca, in the Sobova Formation.

DESCRIPTION. The only evidence of a harpidid trilobite at this locality is a very small fragment of the dorsal fringe lamella. There is a narrow, raised rim inside which the concave surface is traversed by several thin ridges representing the genal caeca. Some of the latter are directed radially but others are more unevenly distributed. Between the ridges the surface is covered with small pits with a roughly radial arrangement in rows. The material is insufficient for certain generic determination, and it is clearly distinct from the *Harpides* sp. of locality B.651, but some comparison may be made with *Harpides rugosus* (Sars & Boeck 1838) from the Ceratopyge Limestone, Tremadoc Series, of Norway as redescribed by Henningsmoen (1959 : 166). In particular Henningsmoen's pl. 2, fig. 9 shows both radial and anastomosing genal caeca that are broadly similar to those now illustrated.

Family **TRINUCLEIDAE** Hawle & Corda, 1847

Trinucleid gen. et sp. indet.

(Pl. 2, figs. 2, 6, 8)

Figured specimens. BM. It.7898 (Pl. 2, figs. 2, 8), It.7901 (Pl. 2, fig. 6).

Locality and horizon. B.651 at the Sobova Valley section, in the limestone member of the Sobova Formation.

Description. Evidence of trinucleid trilobites from the Sobova Formation is, unfortunately, scarce and so far comprises only the two poorly preserved fragments of cephalic fringe now illustrated. The more informative specimen, It.7898, shows what appears to be truly part of the marginal suture bounding a single arc of E pits, whilst the girder is well developed and there are at least three I arcs. There is little variation in pit size and the precise orientation of the specimen is debatable but the I pits exhibit a semblance of radial arrangement, with a few pits in interradial positions. Whether one regards the specimen as representing part of the left half or the right half of the cranidium, the I radii meet the girder at an acute angle. It.7901, although even less complete, shows two E arcs, as inferred from their position adjacent to the convex curvature and asymmetrical cross-section of the strongly developed girder. The I arcs of this specimen are not preserved.

Discussion. The material is insufficient for confident assignment, but the presence of even one E arc is sufficient to eliminate such early Ordovician genera as *Myttonia* Whittard 1955 and *Hanchungolithus* Lu 1954, both of which have a marginal girder and are known from the Arenig Series of the Anglo-Welsh area and the Tethyan region. Also in the Anglo-Welsh area Whittard (1966) described an association of *Lordshillia*, *Cochliorrhoe* and *Incaia* from the lower Arenig Series of the Shelve Inlier. Of these, *Incaia simplicior* Whittard (1966 : 274) has since been made the type species of a new genus *Anebolithus* Hughes & Wright (1970 : 688) and is clearly distinct from the Sobova specimen, as is *Lordshillia confinalis* Whittard (1966 : 277), in which the fringe is of relatively simple type, having only arcs E_1 and I_{1-2}. *Cochliorrhoe*, type species *C. inquilinum* Whittard (1966 : 278), has been placed in synonymy with *Bergamia* Whittard, 1955 by Hughes (1971 : 139). The latter genus has been redefined by Hughes (1971 : 120) as, *inter alia*, ' having E_1 fully and E_2 variably developed ; up to six I arcs present laterally '. Such a diagnosis would appear appropriate for the Turkish specimens, as far as can be judged, but additional material is required.

Family **CHEIRURIDAE** Hawle & Corda, 1847

Cheirurid genus and species undetermined

(Pl. 2, fig. 5)

FIGURED SPECIMEN. BM. It.7900.

LOCALITY AND HORIZON. B.651 at the Sobova Valley section, in the limestone member of the Sobova Formation.

DESCRIPTION. An isolated right librigena is the only example of a cheirurid trilobite yet found in the Sobova Formation. The adaxial portion declines steeply from the eye towards a deep, broad, lateral border furrow which separates it from the upturned, slightly bevelled lateral border. The external surface of the border is finely granulated but the remainder of the librigena is covered with well-spaced pits. The anterior branch of the facial suture, though incomplete, appears to run abaxially in a gentle curve for about half its length and then turns adaxially. The posterior branch arches backwards more strongly to meet the lateral cephalic margin at a sharply acute angle.

DISCUSSION. Generic identification is difficult with such limited material but the specimen closely resembles the librigenae of *Pseudosphaerexochus hemicranium* (Kutorga, 1854 : 112, pl. 1, figs. 2a–c ; see also Schmidt, 1881 : 171, pl. 10, figs. 1–4 ; pl. 16, figs. 22–27) from the Middle Ordovician of Estonia. *Pseudosphaerexochus* sensu stricto has not been reported from an horizon in the Ordovician as early as that represented by the Sobova Formation, but species of the subgenus *Pseudosphaerexochus* (*Pateraspis*) have been described from Arenig strata in Balto-Scandia, although the type species, *Cheirurus pater* Barrande 1872 (see Prantl & Přibyl, 1947 : 30–32), is from the Šárka Beds, Llanvirn Series, in Bohemia, where another species is stated to occur higher in the Dobrotivá Beds of Llandeilo age. The librigenae of *P.* (*P.*) *pater* are generally similar to those of the Sobova specimen. The corresponding structures have not been described for either of the two known Balto-Scandinavian species but, judging from the course of the facial sutures, comparison may be made with *P.* (*P.*) *inflatus* V. Poulsen (1965 : 104, pl. 9, figs. 1–9), from the *Cyclopyge stigmata* Zone of Bornholm, rather than with *P.* (*P.*) *praecursor* Regnéll sp. (1940 : 5, 12, pl. 1, fig. 6) from the Planilimbata Limestone of Öland, in which the posterior branch of the facial suture appears to be markedly longer.

Family **PLIOMERIDAE** Raymond, 1913

Genus ***PLIOMERINA*** Chugaeva, 1956

TYPE SPECIES. *Pliomera Martellii* Reed, 1917.

Pliomerina sp.

(Pl. 2, figs. 3, 13)

FIGURED SPECIMEN. BM. It.7899.

LOCALITY AND HORIZON. C.429, 1·5 km east of Kızılca, in limestones of the Sobova Formation.

DESCRIPTION. A fragmentary glabella is figured here as internal mould and latex cast. There is a smooth median band about one-third the glabellar breadth and only the two anterior pairs of lateral glabellar lobes remain but it may be seen that the 1p glabellar furrows are deep and transversely straight. The 2p glabellar furrows are generally similar but curve backwards gently from the axial furrows, whilst the 3p furrows are straight and deep, diverging forwards at an obtuse angle. Of the lateral glabellar lobes so delimited, the 2p pair are transversely rectangular and smaller than the subrectangular 3p pair. Although incomplete, the glabellar outline appears to broaden forwards as far as the 3p lobes. The frontal glabellar lobe is approximately quadrant-shaped, its anterior margin broadly arched forwards in plan ; traces of a small median depression on the internal mould just behind the preglabellar furrow may not be an original feature as there is no evidence of such a structure on the external mould, though the latter is incomplete. The external surface is ornamented with a few scattered tubercles.

DISCUSSION. In spite of its fragmentary nature, the specimen is clearly of pliomerid type. There is no incised median indentation of the frontal glabellar lobe as in *Pliomera*, nor are the 3p glabellar furrows sited sufficiently far forwards to match those of *Pliomera* or *Pliomerops* and several related genera. Closer comparison may be made with the type species of *Pliomerina*, *P. martellii* (Reed 1917 : 55, pl. 8, figs. 15, 16), which the present fragment resembles in the size and shape of the 2p, 3p and frontal glabellar lobes and, particularly, in the transverse direction of the 1p and 2p glabellar furrows. Australian occurrences of *Pliomerina* have recently been described by Webby (1971), all from strata equated with part of the Caradoc Series and therefore considerably younger than the Kızılca specimen. However, *P. martellii* was described originally from strata in southern China said to be of upper Llanvirn age and in association with trilobites that exhibit marked Baltic affinities (Reed 1917 : 67 ; Brown 1950 : 322 *et seq.*).

Family **PTERYGOMETOPIDAE** Reed, 1905

Genus ***PTERYGOMETOPUS*** Schmidt, 1881

TYPE SPECIES. *Calymene sclerops* Dalman, 1827.

Pterygometopus ? sp.

(Pl. 3, figs. 1–3, 7, 14)

FIGURED SPECIMENS. BM. It.7906 (Pl. 3, figs. 1–3), It.7912 (Pl. 3, figs. 7, 14).

LOCALITY AND HORIZON. B.651, at the Sobova Valley section, in the Sobova Limestone member of the Sobova Formation.

DESCRIPTION. An isolated glabella and occipital ring have a combined median length of 6·5 mm ; the frontal glabellar lobe has a maximum breadth of 4·8 mm (estd) whilst that of the occipital ring is 3·0 mm (estd). There are three well-defined pairs of lateral glabellar lobes, delimited by deep, slot-like glabellar furrows that leave a median band approx. 1·2 mm wide. The glabella is bounded by axial furrows that diverge forwards at about 25 degrees from the occipital furrow to the

3p glabellar furrows and then become more splayed in plan. The 1p glabellar lobes are small, defined anteriorly by deep, transversely straight 1p furrows. The 2p glabellar lobes are slightly larger, subquadrate in plan, and the deep, narrow (*exsag.*) 2p glabellar furrows run only slightly forwards adaxially. The 3p lobes and furrows are similar to those of the 2p pairs. Between the occipital furrow and the 2p glabellar furrows the glabellar outline is parallel-sided, but farther forwards it expands sharply so that the dominantly large frontal glabellar lobe is almost twice as broad (*tr.*) as the base of the glabella. The frontal lobe is rather less than three times as broad as long, steeply declined frontally (see Pl. 3, fig. 2), and in plan is markedly well rounded, resulting in an axe-like outline. The occipital ring, although incompletely preserved, becomes narrower (*exsag.*) laterally and extends slightly beyond the sides of the glabella. In anterior and lateral views it can be seen to stand notably higher than the top of the glabella (see Pl. 3, figs. 2, 3), and there is a low median occipital tubercle. The front of the glabella is circumscribed by a narrow, shallow preglabellar furrow, immediately in front of which is a thin strip of anterior border, terminated by the frontal portion of the facial suture. The remainder of the cephalon is not preserved.

The surface of the exoskeleton is seen on only part of the posterior half of the glabella, where it is covered with closely grouped small tubercles that give a coarsely granulated appearance.

DISCUSSION. This single fragmentary specimen poses problems of identification that can be resolved only by further collecting. Superficially the outline of the glabella resembles that of *Ormathops*, but the large, axe-shaped frontal glabellar lobe, the course of the 2p and 3p glabellar furrows, which run slightly forwards adaxially, and the almost equisized 2p and 3p glabellar lobes, show this cannot be the case. All these features are found to some degree in *Pterygometopus*, a genus redescribed by Whittington (1950 : 538) who restricted it to forms resembling the type species, *P. sclerops* (Dalman) (see also Schmidt 1881 : 77) from the Expansus or lower Raniceps Limestone, uppermost Arenig or lowest Llanvirn Series of Sweden, and *P. trigonocephalus* (Schmidt 1881 : 81) from strata of approximately similar age in Russia. The axial furrows of the Turkish specimen do not bend adaxially in the vicinity of the occipital ring as do those of *P. sclerops*, and the frontal glabellar lobe is shorter than that of the Swedish species, though not so long as that of *P. trigonocephalus* from the Vaginatum Limestone of Pawlowsk (see Schmidt 1881 : pl. 1, figs. 9–12 only). The last-named species probably affords the closest comparison because it, too, has a median tubercle on the occipital ring, the posterior halves of the axial furrows are slightly divergent forwards, and the axial furrows are more nearly parallel-sided posteriorly.

A single fragmentary pygidium (Pl. 3, figs. 7, 14) has the axis bounded by deep, straight axial furrows that converge gently to a bluntly rounded tip. In addition to the articulating half-ring there are five well-defined axial rings, separated by continuous, transversely straight ring furrows, followed by two smaller rings which are defined only medially. The tip of the pygidium is not preserved but as far as can be judged the pleural regions carry five pairs of pleurae which become progressively more strongly curved back from first to fifth. The pleurae are separated by interpleural furrows that appear to extend to, or almost to, the pygidial margin, and each pleura is divided into two equal bands, the posterior of which is slightly the thicker, by a pleural furrow that dies out approximately two-thirds of the distance from the axial furrow to the margin. Closely grouped small tubercles are preserved on part of the dorsal surface. The pygidium generally resembles that of *Pterygometopus sclerops* illustrated by Whittington (1950 : pl. 69, fig. 1) but the pleural and interpleural furrows have been exaggerated by longitudinal compression. The relative length of the axis and the form of the hindmost pleurae would appear to rule out a calymenid and the specimen, like the above glabella, is referred only questionably to *Pterygometopus*.

Family **PTYCHOPARIIDAE** Matthew, 1887
Subfamily **EULOMINAE** Kobayashi, 1955
Genus ***EULOMA*** Angelin, 1854

TYPE SPECIES. *Euloma laeve* Angelin, 1854.

Subgenus ***LATEULOMA*** nov.

TYPE SPECIES. *Euloma* (*Lateuloma*) *latigena* sp. nov.

DIAGNOSIS. Subgenus of *Euloma* distinguished by the following features: palpebral lobes small, set well back, opposite 1p glabellar furrows and separated from glabella by wide fixigenae ; narrow eye-ridges run gently backwards abaxially from axial furrows just in front of 2p glabellar furrows to anterior ends of palpebral lobes ; anterior border of cranidium curves strongly forwards in plan from points immediately in front of palpebral lobes and well behind transverse line through preglabellar furrow; numerous small pits arranged along frontal side of anterior border furrow.

DISTRIBUTION. Arenig Series of southern Turkey.

Euloma (Lateuloma) latigena sp. nov.

(Pl. 3, figs. 5, 6, 8–11)

DIAGNOSIS. As for subgenus.

HOLOTYPE. BM. It.7910 (Pl. 3, fig. 8).

PARATYPES. BM. It.7908 (Pl. 3, fig. 5), It.7909 (Pl. 3, figs. 6, 10, 11), It.7911 (Pl. 3, fig. 9).

LOCALITY AND HORIZON. The type material is from locality C.429, 1·5 km east of Kızılca, in the Sobova Formation, but the species occurs also at C.432, 0·75 km west of the same village.

DESCRIPTION. The species is represented mostly by isolated cranidia. The median length is almost two-thirds the maximum breadth and the overall outline is broadly semielliptical. Half the cranidial length is occupied by the glabella, slightly broader than long, its outline bluntly rounded frontally. There are two pairs of glabellar lobes, the 1p pair slightly the larger and of ' cat's ear ' shape reminiscent of the corresponding structures in calymenids ; the deep 1p glabellar furrows curve strongly back adaxially towards but do not reach the occipital furrow. The 2p lobes are subrectangular in plan, broadly divergent forwards, and bounded by deep, straight 2p glabellar furrows. The sides of the glabella converge forwards only very slightly as far as the 2p furrows, at which point there is a marked ' step ' or constriction in the outline, which narrows abruptly to three-quarters of the basal breadth. The sides of the glabella are defined by deep, broad axial furrows, continuous frontally with the preglabellar furrow, which becomes slightly shallower at the sagittal line. The occipital ring has a median length (*sag.*) one-third that of the glabella, and is separated from the latter by a faintly curved occipital furrow, convex forwards, that is set a little in advance of the deep, transversely straight posterior border furrow. A pronounced median tubercle is situated just in front of centre of the occipital ring. The posterior border is incompletely known but terminates laterally just beyond the outer edge of the palpebral lobes. At the sagittal line the preglabellar field and anterior border have a combined length (*sag.*) two-thirds that of the glabellar length ; about half this measurement is occupied by the preglabellar field, which passes laterally without a break into the fixigenae. A broad (*sag.*), shallow anterior border furrow separates the preglabellar field from a conspicuous anterior border of thickened appearance which is strongly convex forwards in plan and extends posterolaterally so that a line joining the extremities would pass through the glabella just in front of the 2p glabellar furrows. Several conspicuous perforations are distributed along the front side of the anterior border furrow ; their positioning and size are not uniform and their number, difficult to determine precisely because of incomplete preservation, is estimated to range from 16 to 18. The incomplete evidence suggests that the pits may not be arranged symmetrically about the sagittal line. The palpebral lobes are reniform in outline, abaxially convex, bounded by deep, curved palpebral furrows which turn abaxially around the ends of the lobes. The length of the palpebral lobes is almost half that of the glabella, and they extend forwards from immediately in front of the posterior border furrow to just behind a transverse line through the outer ends of the 2p glabellar furrows. The distance between each palpebral lobe and the adjacent axial furrow is almost three-quarters of the basal glabellar breadth ; the fixigenae are consequently relatively large, of depressed form, and are transversed by a pair of thin, low eye-ridges that run in gentle curves, convex forwards, from the palpebral furrows near the frontal ends of the palpebral lobes to meet the abaxial margins of the axial furrows just forward of the 2p glabellar furrows. Because of the markedly posterolateral position of the extremities of the anterior border, which terminate abaxially just outside the line of the palpebral lobes, the branches of the facial suture are correspondingly short and the librigenae must have been notably small. The anterior branches diverge forwards strongly and then turn forwards through almost a right-angle as they cut the anterior border ; the posterior branches are incompletely known but converge gradually upon the posterior border furrow.

The pygidium is known only from a fragment of external mould (Pl. 3, fig. 5); although incomplete, the estimated length is of the order of 4·5 mm and the breadth 11·0 mm. The outline is transversely semielliptical and the straight anterior margin curves posterolaterally on the outer halves of the pleural fields. There is a thickened border which broadens anterolaterally, separated by a shallow border furrow from pleural fields which show evidence of two pairs of broad (*exsag.*) pleural furrows and one pair of faint interpleural furrows. The straight-sided axis has a tapered outline; only the anterior half is preserved, on which are two axial rings separated by transversely straight ring furrows.

DIMENSIONS (in mm, IM = internal mould, EM = external mould).

	It.7909	It.7910	It.7911
Median length of cranidium	6·5 (IM)	4·8 estd (EM)	6·7 estd (IM)
Breadth across palpebral lobes	9·0 estd (IM)	6·6 estd (EM)	8·6 estd (IM)
Length of glabella	3·4 (IM)	2·5 (IM)	3·2 (IM)
Basal breadth of glabella	3·5 (EM)	2·5 (IM)	3·5 (IM)

DISCUSSION. The type species of *Euloma* sensu stricto, *E.* (*E.*) *laeve* Angelin, 1854, occurs in much of the Upper Planilimbata Limestone, Lower Arenig Series, of Sweden according to Tjernvik (1956: 274, pl. 11, figs. 1–3, text-fig. 45B) whose illustrations show that the new subgenus may be separated on the basis of the smaller eyes; broader fixigenae with eye-ridges running slightly backwards abaxially; and in particular by the large size and curved posterolateral extensions of the anterior border, so that the librigenae, although not yet recovered, must have been exceedingly small.

Occupying a position intermediate between *E.* (*Euloma*) and *E.* (*Lateuloma*) is the subgenus *E.* (*Proteuloma*) founded by Sdzuy (1958: 269) on *Conocephalites geinitzi* Barrande, 1868, a species from the Lower Tremadoc of Bavaria and southern France. Illustrations of *E.* (*P.*) *geinitzi* published by Sdzuy (1955: pl. 3, figs. 77–89, pl. 4, figs. 90–92; 1958: pl. 3, figs. 4, 5, 7–17) show that the new Turkish species differs in the following respects: (a) the outline of the glabella is relatively shorter and broader, becoming more constricted in front of the 2p glabellar furrows; (b) in plan view the anterior border is longer (*tr.*), much more strongly curved back, and terminates behind a transverse line through the 2p glabellar furrows, so that the anterior branches of the facial suture are both shorter and more strongly divergent forwards – in *E.* (*P.*) *geinitzi* the short (*tr.*) anterior border terminates laterally in front of a transverse line drawn through the preglabellar furrow at the sagittal line; (c) the better defined palpebral lobes face laterally rather than anterolaterally, and are sited proportionately closer to the posterior border furrow, so that the posterior branches of the facial suture are shorter and the posterolateral areas of the fixigenae smaller.

The British Tremadoc species *Conocoryphe monile* Salter (1873: 32) from the Shineton Shales of Shropshire, later assigned to *Euloma* (see especially Lake 1940: 303, pl. 43, figs. 2–9), was subsequently placed in *E.* (*Proteuloma*) by Sdzuy (1958: 269–271). Some of Lake's illustrations show the anterior border of *E.* (*P.*) *monile*, and that of the slightly older subspecies *E.* (*P.*) *monile praemonile* Lake, unusually well curved back posterolaterally, but according to Sdzuy's restoration (1958 : text-fig. 3), the anterior border does not extend behind a transverse line through the front of the glabella. Most of the specimens illustrated show the anterior border of *E.* (*P.*) *monile* much shorter (*tr.*) and less arched forwards in plan than that of *E.* (*L.*) *latigena*, and the palpebral lobes of the Shropshire species set farther forwards and proportionately closer to the glabella. However, certain cranidia collected by me from the Shineton Shales have relatively wide fixigenae and the anterior border extends behind the front of the glabella, so that the specimens have more in common with *E.* (*Lateuloma*) than with Sdzuy's reconstruction. The Shropshire material is dorsally compressed to varying degrees and a more detailed comparison must await the redescription of *Euloma monile*.

The cranidium of *Euloma kazachstanica* Balashova (*in* Chernysheva 1960 : pl. 10, fig. 5), from the Tremadoc of Kazachstan, appears to have the eyes set relatively far from the glabella and only a short distance in front of the posterior border furrow. This species may belong to *E.* (*Lateuloma*) but the illustration is insufficient for detailed comparison.

Family **KOMASPIDIDAE** Kobayashi, 1935

Genus ***CAROLINITES*** Kobayashi, 1940

Type species. *C. bulbosa* Kobayashi, 1940.

Subjective synonyms. *Dimastocephalus* Stubblefield, 1950 ; *Keidelia* Harrington & Leanza, 1957.

Carolinites sp.

(Pl. 3, figs. 4, 12, 13)

Figured specimen. BM. It.7907.

Locality and horizon. B.651 at the Sobova Valley, in the limestone member of the Sobova Formation.

Description. A single incomplete cranidium has the glabella slightly less than one and a half times as broad as long and markedly convex both longitudinally and transversely. The glabellar outline is subquadrate, its posterior margin transversely straight and the sides subparallel, indented basally by a pair of small subelliptical lobes which project slightly beyond the sides. The lobes are apparently separated from the main body of the glabella by the adaxial curvature of the axial furrows and are difficult to delimit from the fixigenae, into which they merge. Ross (1951 : 83) suggested that such structures, for which he preferred the term 'preoccipital lobes', did not form part of the glabella, and this view may well prove to be correct. One may also note that the lobes are sited beyond the ends of the occipital ring. The glabellar outline is well rounded anterolaterally, but frontally is almost transversely straight, with a broad, shallow median indentation that produces a slightly bilobed appearance. There is no preglabellar field and the glabella is separated by a deep, rounded furrow from the small anterior border which is sharply upturned and has a transverse breadth approximately equal to that of the glabella. The occipital ring is large, almost parallel-sided, and extends laterally about level with the mid-points of the ' pre-occipital lobes '. The palpebral lobes, although incomplete, are bounded adaxially by almost straight, low ridges that converge forwards at slightly more than 60 degrees for the anterior two-thirds of their length ; posteriorly they curve backwards slightly and are only gently convergent forwards immediately in front of the posterior border furrow. The fixigenae are low, flattened and subtriangular in outline, narrowing towards the extremities of the anterior border. The incomplete posterior border is bounded by a transversely straight posterior border furrow in-line with the occipital furrow. No traces of ornamentation have been detected.

The remainder of the exoskeleton is not known.

DIMENSIONS. Length of cranidium = 6·0 mm, length of glabella = 4·5 mm, median breadth of glabella = 5·2 mm.

DISCUSSION. The cranidium most resembling the Sobova species is that of *Carolinites killaryensis utahensis* Hintze (1952 : 145, pl. 20, figs. 10–13), from Zone M of Utah, which agrees in glabellar proportions, the frontal median indentation of the glabella and the size of the pre-occipital lobes ; the only apparent difference is in the size of the fixigenae which are slightly narrower. *C. killaryensis* was described (as *Dimastocephalus*) from rocks of probably Arenig age in western Ireland by Stubblefield (1950 : 345, pl. 2, figs. 1–7). The glabella, though of similar type to the present material, has the front of the glabella broadly rounded, whilst a more conspicuous difference is the relatively large size of the fixigenae, which are broader than in any other described species of the genus.

The type species *Carolinites bulbosus* Kobayashi (1940 : 70, pl. 12, figs. 6–7), from the Lower Ordovician of Tasmania, is in need of revision and comparison is difficult. One may note, however, that in his diagnosis of the genus Kobayashi emphasized the absence of glabellar furrows. The glabella of *C. bulbosus* appears to be more nearly parallel-sided than that of the Turkish specimen, with the ' pre-occipital lobes ' set outside the line of the axial furrows.

The cranidium from the Sobova Formation also strongly resembles that of *Carolinites genacinaca* Ross (1951 : 84, pl. 18, figs. 25, 26, 28–36) from Zone J of northeastern Utah, differing only in the indentation of the front of the glabella and the stronger turning backwards of the palpebral lobes, so that the fixigenae are slightly narrower. *C. genacinaca* as reported from Zone J of central Utah by Hintze (1952 : 145, pl. 20, figs. 7–9) shows the median indentation and the pygidium is proportionately longer than that illustrated by Ross, with less convergent lateral margins.

Carolinites [*Keidelia*] *macrophthalmus* (Harrington & Leanza 1957 : 141, Fig. 59, 1–2), from the Caradoc Series of Argentina, is an unusually young member of the genus and the only described species not of Lower Ordovician age. The anterior border is similar to that of the Turkish form, but the Argentinian trilobite may be distinguished by its relatively narrower glabella, the frontal lobe of which lacks a median indentation, the larger pre-occipital lobes and by the stronger abaxial curvature of the palpebral lobes. The Caradoc age of this species seems debatable and elsewhere Harrington & Leanza (1957; 214) denote the type locality as being of Llanvirn age.

Family **REMOPLEURIDIDAE** Hawle & Corda, 1847

Genus ***APATOKEPHALUS*** Brøgger, 1896

TYPE SPECIES. *Trilobites serratus* Boeck, 1838.

Apatokephalus sp.

(Pl. 2, fig. 14; Pl. 4, fig. 7)

FIGURED SPECIMENS. BM. It.7915 (Pl. 2, fig. 14), It.7919 (Pl. 4, fig. 7).

LOCALITY AND HORIZON. Locality B.651 at the Sobova Valley, in the Sobova Limestone member of the Sobova Formation.

A fragment of the right half of the glabella (It.7915) shows the characteristic outline, broad and rounded posteriorly but markedly constricted in front of the 2p glabellar furrow. The latter is apparently long (*tr.*) and straight but may have been exaggerated by crushing whilst the 1p glabellar furrow is shorter, curved and does not attain the glabellar margin. The exoskeleton shows numerous small tubercles on both outer surface and internal mould.

The ventral side of an incomplete left librigena shows the librigenal spine arising well in front of the genal angle and forming an acute-angled librigenal notch. The spine is long, gently curved, directed strongly back posterolaterally, and its surface carries several subparallel, longitudinal ridges.

DISCUSSION. *Apatokephalus* has an almost cosmopolitan distribution and is found only in rocks of Tremadoc or Arenig age. The type species, *A. serratus* (Boeck) from the eponymous zone of the Tremadoc Series of Norway, has been redescribed from a corresponding horizon in Sweden by Tjernvik (1956 : 204, pl. 2, figs. 7, 8, text-fig. 32A) whose illustrations show that the Turkish species has the posterior end of the palpebral lobe flexed strongly inwards and slightly forwards, whereas that of *A. serratus* is evenly curved overall. The Sobova cranidium may, perhaps, be better compared with that of *A. incisus* Dean (1966 : 339, see especially pl. 20, figs. 1, 2 ; pl. 21, fig. 3), from the Arenig Series of southern France, which has similar granular ornamentation but has 1p glabellar furrows that are both shorter (*tr.*) and less strongly curved.

The Turkish librigena has a librigenal notch similar to that found on *A. serratus* as illustrated by Tjernvik (1956 : text-fig. 32A) though not as shown for the same species by Whittington (*in* Moore, 1959 : Fig. 243, 2a). Again, comparison may be made with *Apatokephalus incisus* (Dean 1966 : pl. 20, figs. 5, 6 ; pl. 21, fig. 1).

Family **BATHYURIDAE** Walcott, 1886

Genus ***AGERINA*** Tjernvik, 1956

TYPE SPECIES. *Agerina erratica* Tjernvik, 1956.

Agerina pamphylica sp. nov.

(Pl. 4, figs. 1, 2, 4–6; Pl. 5, fig. 6)

DIAGNOSIS. Species of *Agerina* with subrectangular glabella divided into three unequal glabellar lobes and slightly expanded frontal lobe by glabellar furrows that become shorter and less curved from 1p to 3p. Semielliptical palpebral lobes extend from opposite centre of 1p lobes to just in front of 2p furrows. Anterior border narrow (*sag.*). Surface of exoskeleton pitted. Sub-semielliptical pygidium ends in blunt point and has two fused pleurae visible; straight-sided axis has four rings and small, blunt terminal piece.

LOCALITY AND HORIZON. B.651 at the Sobova Valley section, in the limestone member of the Sobova Formation.

HOLOTYPE. BM. It.7914 (Pl. 4, fig. 2).

PARATYPES. BM. It.7913 (Pl. 4, fig. 1), It.7916 (Pl. 4, fig. 4), It.7917 (Pl. 4, fig. 5), It.7918 (Pl. 4, fig. 6), It.7928 (Pl. 5, fig. 6).

DESCRIPTION. The species is known only from isolated cranidia and pygidia. The convex glabella is elongated, subrectangular in outline, with gently curved, abaxially convex sides converging slightly at the 3p glabellar furrows, in front of which the subquadrate frontal glabellar lobe expands slightly until as broad as, or a little broader than, the rest of the glabella. There are three pairs of glabellar lobes. The 1p pair occupy one-quarter to one-third of the length of the glabella and are bounded by 1p glabellar furrows that curve inwards and back and terminate opposite or just behind the centre of the 1p lobes. The 2p glabellar furrows run inwards almost transversely and are very slightly curved, convex forwards. The 2p glabellar lobes thus delimited equal just over one-fifth of the length of the glabella and are a little longer (*exsag.*) than the 3p lobes, in front of which the 3p glabellar furrows are shorter (*tr.*) and straighter than the 2p furrows. The foregoing notes on the glabellar furrows apply to the internal mould, upon which they are narrow and incised; on the external surface of the exoskeleton the furrows appear shallower and broader (see Pl. 4, fig. 4 and Pl. 5, fig. 6), and the unfurrowed median band occupies about half the glabellar breadth. The largest cranidia show the glabella expanding forwards only slightly in front of the 3p glabellar furrows, but on the smallest example available (Pl. 5, fig. 6) the corresponding expansion is more pronounced. The glabella is bounded frontally by a narrow (*sag.*), raised anterior border from which it is separated by a deep, narrow furrow that merges with the equally deep and narrow axial furrows. The occipital furrow is narrow (*sag.*), transversely straight and of only moderate depth, whilst the occipital ring has not been found completely preserved. The palpebral lobes are elongated, semielliptical in plan, situated only a short distance outside the axial furrows and extend from opposite the centre of the 3p glabellar lobes until opposite the centre of the 1p lobes.

The palpebral lobes themselves are flattened dorsally and show no palpebral furrows. From them the anterior branches of the facial suture diverge forwards a little more strongly than do the axial furrows, delimit very small, triangular anterior halves of the fixigenae, and run in almost straight lines to the anterior border ; there they turn adaxially through almost a right-angle and meet frontally in a gentle curve in front of and below the top of the anterior border. The remainder of the fixigenae and the posterior branches of the facial suture are not preserved.

The anterior half of a cranidium figured here as a latex cast (Pl. 4, fig. 4) shows the surface of the exoskeleton, excluding furrows, covered with closely spaced perforations. Similar perforations are seen on the glabella of a very small cranidium (Pl. 5, fig. 6), but it is not clear whether in either case this ornamentation extends on to the anterior border.

The pygidium is a little more than twice as broad as long, moderately convex and transversely semielliptical in outline, slightly obtuse posterolaterally and ending in a bluntly pointed tip. The axis stands higher than the pleural regions, its front occupies one-third of the pygidial breadth, and the straight sides converge gently to the blunt tip. In addition to the large articulating half-ring there are four almost equisized axial rings, separated by transversely straight ring furrows, and a short terminal piece. The plump pleural fields pass laterally into a broad (*tr.*), steeply declined border which carries a conspicuous ornamentation of thin, anastomosing ridges and runs immediately behind the tip of the axis. Each pleural field has a conspicuous anterior half-rib delimited by a deep, interpleural furrow that curves gently backwards abaxially as far as the lateral border. Behind is a further conspicuous rib, bounded by a deep pleural furrow and bearing a faint interpleural furrow, but beyond this point there are only faint traces of additional furrows.

DIMENSIONS (in mm, IM = internal mould, EM = external mould).

	It.7913	It.7914	It.7917	It.7918	It.7928
Length of glabella	2·5 estd (IM)	2·6 (IM)	–	–	2·0 (EM)
Max. breadth of glabella	2·0 (IM)	1·8 (IM)	–	–	1·4 (EM)
Breadth across palpebral lobes	–	3·2 estd (IM)	–	–	2·4 (EM)
Length of pygidium	–	–	1·3 (EM)	1·6 (EM)	–
Breadth of pygidium	–	–	3·0 (EM)	4·1 (EM)	–
Length of axis	–	–	1·1 (EM)	1·3 (IM)	–
Frontal breadth of axis	–	–	1·1 (EM)	1·2 (EM)	–

DISCUSSION. The type species *A. erratica* Tjernvik (1956 : 198, pl. 1, figs. 24–26) is of lower Arenig age and comes from the Upper Planilimbata Limestone of Sweden. Like *A. pamphylica* it has faint glabellar furrows but the glabellar outline is proportionately broader, with the frontal lobe more convex forwards in plan. The palpebral lobes of *A. erratica* are set slightly farther forwards and the anterior border appears to be smaller. The pygidium of the Swedish species is shorter and tapers to a blunt point, the tip of the axis is better defined, and there are only three axial rings in addition to the terminal piece. Both species have an unfurrowed pygidial border ornamented with terrace-lines subparallel to the margin. *Agerina praematura* Tjernvik (1956 : 200, pl. 1, figs. 22, 23) has a glabellar outline very like that of *A. pamphylica*, but the glabellar furrows are more deeply incised and there is a low median carina. The pygidial outline, though generally similar to that of the Turkish species, is relatively shorter and the narrower border is apparently delimited by a shallow furrow. There is no evidence of the pitted ornamentation found on the cephalon of *A. pamphylica*, and the pygidium of the latter lacks the granulated surface described by Tjernvik. *A. praematura* is the oldest described species and comes from the Ceratopyge Limestone, upper Tremadoc Series, of Sweden.

Proetus Wöhrmanni Schmidt (1907 : 61, pl. 1, fig. 12 ; pl. 3, fig. 10), from Stufe B_{2b} of the east Baltic region, was assigned to *Agerina* by Tjernvik (1956 : 199) who distinguished it from *A. erratica* by its lack of genal spines and by its trapezoidal, as opposed to triangular, rostral plate. As far as can be judged from Schmidt's illustrations, *Agerina woehrmanni* has a slightly broader glabellar outline than *A. pamphylica* ; the glabella is more constricted at the glabellar furrows ; the 3p glabellar lobes are smaller ; and the frontal glabellar lobe is more rounded in plan. Tjernvik pointed out that Schmidt's species is younger than *A. erratica*, but nevertheless it is no later than Arenig in age and the genus is not known outside the late Tremadoc and Arenig Series.

A small pygidium, It.7921 (Pl. 4, fig. 9), from the type locality of *Agerina pamphylica* has the tip of the axis slightly longer and better defined than that of the new species, whilst the pleural regions, on which are visible two fused pleurae followed by small unfurrowed areas, are bounded by a slightly raised border that is ornamented with terrace-lines. The surface of the exoskeleton shows pitting like that of *A. pamphylica* but in other respects the specimen differs from the pygidia ascribed to that species. The even curvature of the margin and the slightly raised border recall the pygidium of *Agerina praematura* Tjernvik (1956 : pl. 1, fig. 23), but the latter has a broader, less well-defined axis and granulated surface. For the present this specimen is questionably referred to *Agerina* ?

Genus ***PSEUDOPETIGURUS*** Prantl & Přibyl, 1948

TYPE SPECIES. *Cheirurus Hofmanni* Perner, 1900.

Pseudopetigurus cf. ***hofmanni*** (Perner)

(Pl. 5, figs. 13, 14, 16)

1900 *Cheirurus Hofmanni* Perner, pp. 3, 13, pl. 1, figs. 1–5, text-fig. 1.
1948 *Pseudopetigurus hofmanni* (Perner), Prantl & Přibyl, p. 18, pl. 3, figs. 2–4, text-figs. 7, 8.

FIGURED SPECIMEN. BM. It.7931.

LOCALITY AND HORIZON. B.651 at the Sobova Valley section, in the limestone member of the Sobova Formation.

DESCRIPTION. A single incomplete cranidium has the glabella slightly longer than broad in plan view, standing notably higher than the fixigenae. From the transversely straight occipital furrow the glabella expands forwards to attain, at about mid-point, a maximum breadth of one and a half times the basal breadth ; the glabellar outline then narrows more gradually, forming a tumid frontal glabellar lobe that arches down and backwards to the preglabellar furrow. The axial furrows are narrow and sharply defined, forming an even, continuous curve with the preglabellar furrow. There is no sign of glabellar furrows. The front of the cranidium lacks the anterior border and the anterolateral portions of the fixigenae, but the latter can be seen to curve around at least part of the frontal glabellar lobe. The occipital furrow is deep and broad (*sag.*) on the internal mould and transversely straight, whilst the occipital ring is of uniform breadth (*sag.*) for the most part but narrows a little abaxially where it curves gently forwards and extends laterally just beyond the base of the glabella. The fixigenae lack the abaxial margins and eyes, but posteriorly they are bounded by a deep posterior border furrow which is set slightly behind the line of the occipital furrow. The exoskeleton is preserved on part of the glabella and on what remains of the fixigenae; its surface (see especially Pl. 5, fig. 13) is ornamented with numerous closely grouped granules and interspersed tubercles of larger size which show also on the internal mould. The remainder of the exoskeleton is unknown.

DIMENSIONS. Projected length of cranidium = 11·2 mm estd; max. breadth of glabella = 8·0 mm; basal breadth of glabella = 5·2 mm.

DISCUSSION. Although incomplete, the Turkish cranidium bears a striking resemblance to those figured as *Cheirurus Hofmanni* by Perner (1900 : pl. 1, figs.3–5) and is also of comparable size. Perner (1900 : text-fig. 1) drew particular attention to the unusual ornamentation of the exoskeleton, comprising numerous granules with interspersed larger tubercles, and this was noted also by Prantl & Přibyl (1948 : 17) who reproduced some of Perner's original illustrations. The Sobova cranidium shows virtually identical ornamentation on the outer surface but it is not possible to ascertain whether the four pairs of glabellar muscle impressions described by Prantl & Přibyl (1948, text-figs. 7, 8), presumably from internal moulds, are also present. *P. hofmanni* is from the Komárov Beds, D–$d_{1\beta}$, of Kváň, Bohemia, where it was said by Perner to occur with *Amphion* (now *Pliomerops*) *lindaueri* Barrande. The Komárov Beds are nowadays included by Havlíček (*in* Čepek & Zoubek 1961 : 78) as the upper half of the Klabava Formation, of Arenig age.

Family **LECANOPYGIDAE** Lochman, 1953 ?

Genus ***SOBOVASPIS*** nov.

TYPE SPECIES. *Sobovaspis tuberculata* sp. nov.

DIAGNOSIS. Cranidium strongly convex. Glabella longer than broad with outline slightly expanded posteriorly from subquadrate frontal glabellar lobe. Three pairs glabellar lobes visible; 1p lobes small, narrow, bounded by shallow 1p furrows; 2p lobes poorly defined; only faint traces of third pair. Preglabellar field narrow (*sag.*) and flat; anterior border low and thickened. Palpebral lobes close to and opposite median third of glabella, and steeply declined adaxially. Anterior branches of facial suture divergent forwards; posterior branches gently curved posterolaterally.

DISTRIBUTION. Arenig Series of southern Turkey.

Sobovaspis tuberculata gen. et sp. nov.

(Pl. 4, figs. 3, 8, 10–15)

DIAGNOSIS. As for genus.

HOLOTYPE. BM. It.7920 (Pl. 4, figs. 8, 11, 13).

PARATYPES. BM. It.7922 (Pl. 4, fig. 10), It.7923 (Pl. 4, figs. 12, 14, 15), It.7924 (Pl. 4, fig. 3).

LOCALITY AND HORIZON. Locality B.651 at the section on the northwest side of the Sobova Valley, in the limestone member of the Sobova Formation.

DESCRIPTION. Three fragmentary cranidia and one incomplete librigena are available. The glabella is almost trapezoidal in plan with slightly convex sides converging gently forwards to a frontal glabellar lobe which is sub-rectangular in outline, transversely straight frontally, with rounded anterolateral angles. The axial furrows are deep and broad overall but, particularly in the case of the largest specimen, the lateral margins of the glabella are poorly defined. Although the occipital furrow and occipital ring are not preserved, the glabella is apparently longer than broad in the ratio 4 : 3 (estd), and whilst the transverse convexity is only moderate, the dorsal surface is strongly arched-down frontally. There are three pairs of glabellar lobes which increase in size from front to back of the glabella. The 3p and 2p glabellar furrows are short (*tr.*) and so ill-defined as to be scarcely visible, though apparently directed slightly backwards adaxially. Those of the 1p pair are more conspicuous, deepest at their intersection with the axial furrows, becoming shallower as they curve strongly backwards, and dying out before they attain the occipital furrow. The 1p glabellar lobes thus delimited are small and relatively elongated, approximately one-third of the glabellar length, and each about two and a half times as long as broad. A shallow preglabellar furrow separates the well-defined front of the glabella from the flat preglabellar field which is narrow (*sag.*) medially but broadens abaxially (see Pl. 4, figs. 13, 15) where its boundary with the fixigenae is not clearly delimited. The anterior border is broadest (*sag.*) medially, low and of thickened appearance. The holotype retains a portion of the fixigena adjacent to the eye, which is sited a short distance outside the axial furrow and has a length about one-third that of the glabella. Another specimen (Pl. 14, fig. 10) shows the left palpebral lobe to be of narrow, rim-like form, strongly convex in plan and delimited by a conspicuous palpebral furrow. The anterior branches of the facial suture are strongly curved, running abaxially forwards from the eyes until approximately level with the front of the glabella and then turning adaxially to meet the anterior cephalic margin just outside the line of the axial furrows. One incomplete cranidium shows the left posterior branch of the facial suture. It runs only slightly backwards abaxially in a gentle curve so that the posterior half of the fixigena is narrow (*exsag.*) and subtriangular. The posterior border is incomplete, but it is estimated that the distance from the intersection of suture and posterior cephalic margin to the axial furrow approximately equals the basal glabellar breadth. The surface of the glabella is ornamented with numerous large, low, scattered tubercles ; the intervening spaces carry closely packed, fine granules which are visible only under the microscope and sometimes partially coalesce to form thin ridge-like structures. Large tubercles are more abundant on the two smaller cranidia than on the relatively large holotype. The fine granulation extends on to the preglabellar field and at least part of the fixigenae and anterior border. The frontal portion of the anterior border carries several terrace-lines.

An incomplete left librigena (Pl. 4, fig. 3) is roughly quadrant-shaped and has a well-developed eye platform below which the convex cheek surface curves steeply down to the shallow lateral border furrow. This part of the librigena carries very fine granulation and, particularly just below the eye platform, large tubercles similar to those ornamenting the glabellar surface. In some instances the tubercles are themselves ornamented by groups of small granules. The margin of the lateral border has several conspicuous terrace-lines like those on the anterior border. Only part of the posterior branch of the facial suture remains, but it probably cuts the posterior border a short distance from the presumed genal angle.

The remainder of the exoskeleton is unknown.

DIMENSIONS (in mm).

	It.7920	It.7922	It.7923
Frontal breadth of cranidium	9·0 estd	5·6 estd	4·4
Frontal breadth of glabella	4·2	2·6	2·0
Basal breadth of glabella	6·0 estd	–	–
Distance across palpebral lobes	10·0 estd	8·4 estd	–

DISCUSSION. Although *Sobovaspis tuberculata* is quite distinct from all the genera accompanying it in the Sobova Formation, its assignment to a family is difficult owing to paucity of material and poor preservation, so that the genus is placed only questionably in the Lecanopygidae. The latter family was defined by Lochman (1953 : 889) as : 'Trilobites with opisthoparian subisopygous exoskeleton ; glabella broadly conical to subquadrate, pre-glabellar area present or absent, all furrows narrow and shallow, eyes about medium size, usually opposite center of glabella, fixed cheek-palpebral area very narrow, posterior area strap-like in shape ; free cheek with short slender genal spine. Thorax unknown. Pygidium semicircular, axis wider or narrower than pleural regions, length variable, often with low post-axial ridge, usually 3 axial rings, no border furrow, medium-width border. Outer surface smooth.' Using the criteria of glabellar outline, position of eyes, proportions of fixigenae and course of facial suture, what is known of *Sobovaspis* would certainly fall within the limits of such definition, though the large, abaxially convex palpebral lobes, well-developed anterior border and coarse tuberculation are more doubtful. The type species of *Lecanopyge*, *L. expansa* Raymond (1937 : 1101, pl. 2, figs. 6–8) from the Gorge Formation, Upper Cambrian, at Highgate Falls, Vermont, was shown originally to have three well-defined pairs of glabellar furrows, though Raymond's text stated that they were less distinct than in his illustrations. A more recent diagnosis of the genus by Lochman (*in* Moore, 1959 : O 380, Fig. 287, 1a) noted three faint pairs of glabellar furrows, though her illustration of the type species has only a single pair, delimiting small 1p glabellar lobes, whilst the preglabellar field and anterior border are of equal breadth (*sag.*). Raymond's original account of *Lecanopyge expansa* described the surface of cranidium and pygidium as punctate, whilst very fine granules cover much of the cranidium of *Sobovaspis*. The latter's additional ornamentation of large tubercles also disagrees with the original diagnosis of Lecanopygidae, but since then *Reubenella rex* Lochman (1966 : 543, pl. 62, figs. 19–25) with ' outer surface coarsely granular ' and *Strigigenalis amerada* Lochman (1966 : 543, pl. 62, figs. 26–30, 35) with ' outer surface covered with granules of two sizes ' have been assigned to the family. Both species are from the Arenig Series of Montana.

Family **PHILLIPSINELLIDAE** Whittington, 1950

Genus ***PHILLIPSINELLA*** Novák, 1886

TYPE SPECIES. *Phacops parabola* Barrande, 1846.

Phillipsinella matutina sp. nov.

(Pl. 5, figs. 2–5, 9–11)

DIAGNOSIS. Glabella clavate with frontal lobe almost half median length. Palpebral lobes sited behind centre in relation to glabella. Anterior border forms low rim around front of glabella. Fixigenae small. Surface ornamented with Bertillon pattern of ridges, separated by concentric rows of small pits. Pygidium has well-rounded outline, its posterior margin slightly arched medially. Axis with three rings, traces of fourth ; tip undefined. Pleural fields show two fused pleurae ; border slightly raised.

LOCALITY AND HORIZON. B.651 at the Sobova Valley section, in the limestone member of the Sobova Formation.

HOLOTYPE. BM. It.7926 (Pl. 5, figs. 3, 9).

PARATYPES. BM. It.7925 (Pl. 5, figs. 2, 5, 10), It.7927 (Pl. 5, figs. 4, 11).

DESCRIPTION. The species is represented by three small specimens, two incomplete cranidia and one incomplete pygidium. The glabella is clavate in outline with almost the whole of the anterior half occupied by a frontal glabellar lobe that expands to a breadth equal to three-fifths of the length of the glabella, and projects forwards strongly in a prominent arch. The posterior half of the glabella is mostly parallel-sided but the hindmost portion expands slightly, immediately in front of the transversely straight occipital furrow. The occipital ring is broadest (*sag.*) medially and its posterior margin curves gently forwards abaxially to terminate just beyond the sides of the glabella. There are no distinct glabellar furrows. The frontal glabellar lobe is bounded by a low, rim-like anterior border, from which it is separated by a narrow groove. The anterior border broadens (*exsag.*) slightly at or near its intersection with the frontal ends of the axial furrows. The latter are narrow and deep over their posterior halves, which are set high alongside the glabella, but become shallower as they arch down frontally. The anterior halves of the fixigenae are narrow (*tr.*) and flange-like, and the anterior branches of the facial suture diverge forwards parallel to the axial furrows. Although the palpebral lobes are not preserved, it is clear that they were positioned well behind a transverse line through the centre of the glabella. The posterior halves of the fixigenae, though fragmentary, appear to be small and subtriangular, with the posterior branches of the facial suture curving backwards posterolaterally. The posterior border, again incomplete, is apparently narrower (*exsag.*) than the occipital ring and delimited by an almost transversely straight posterior border furrow. The surface of the glabella is ornamented with a Bertillon pattern of narrow, low ridges, in between which are sited concentric rows of small pits (see especially Pl. 5, fig. 9). No ornamentation is visible on the internal mould.

An incomplete pygidium preserved as the internal mould has an estimated breadth and median length of 2·5 mm and 1·2 mm respectively. The outline is sub-semicircular, becoming more convex posterolaterally, whilst there is a suggestion of a slight median indentation (incompletely preserved) where the posterior margin is slightly arched transversely. The axis tapers gently backwards, bounded by straight axial furrows which terminate abruptly at three-quarters of the pygidial length, and the tip is not defined – apparently an original feature, though minor abrasion cannot altogether be ruled out. The first axial ring furrow is broad (*sag.*) and conspicuous, but the second is much shallower ; there is only a trace of the third, and both it and the fourth ring furrow are indicated by pairs of small, pit-like depressions near the axial furrows. The border of the pygidium forms a slightly raised rim, delimited by a broad, shallow border furrow. The pleural fields show evidence of two fused pleurae, each carrying a conspicuous pleural furrow which curves backwards abaxially to cross the border furrow and merge with the pygidial border.

DIMENSIONS (in mm, IM = internal mould, EM = external mould).

	It.7925	It.7926	It.7927
Median length of cranidium	–	2·2 (EM)	–
Median length of glabella	2·0 (IM)	1·7 (EM)	–
Max. breadth of glabella	1·2 (IM)	0·9 (EM)	–
Basal breadth of glabella	0·8 estd (EM)	0·6 (EM)	–
Max. breadth of pygidium	–	–	2·5 estd (EM)
Median length of pygidium	–	–	1·2 (EM)

DISCUSSION. *Phillipsinella* is best known from its abundance in the middle Ashgill Series, at which horizon *P. parabola* (Barrande), described in detail by Whittington (1950 : 559) and Kielan (1960 : 72), has proved of stratigraphical value in both western and central Europe, but trilobites of similar type evidently had a long Ordovician history, though their systematic relationships are not yet fully understood. Other records include *Phillipsinella parabola* in the Upper Chasmops Limestone (high Caradoc Series) of Ringerike, southern Norway (Størmer, 1953 : 87), whilst in the Caradoc Series of Sweden Thorslund (1948 : 346) noted *P.* cf. *parabola* in the Lower Chasmops Series of Kinnekulle, and Olin (1906 : 78) recorded *P. parabola* from the Upper Ludibundus Beds of Scania. In still older strata is *Phillipsinella* sp. recorded from the Uhaku Stage, Llandeilo Series of Östergötland (Jaanusson 1960 : 234) and Siljan, Sweden (Jaanusson 1963 : 37), and *Phillippsinella* (sic) *borealis* was erected by Kummerow (1927 : 13, pl. 1, figs. 7, 8) on material from an erratic boulder of ' unteren roten Orthocerenkalkes ', supposedly Arenig Series, in East Prussia. Thanks to the courtesy of Dr. K. Diebel of the Geologisch-Paläontologisches Institut of the University of East Berlin, I have been able to examine Kummerow's two syntypes. The cranidium of *P. borealis,* although incomplete, has the glabellar outline much less expanded frontally than that of *P. parabola* and the fixigenae are narrower ; in these respects it approaches closer to *P. matutina,* but the latter has the front of the glabella more strongly convex forwards in plan. The pygidium of *P. borealis* is larger and more quadrate in outline than that of *P. matutina* and the border forms a more distinct brim, but both appear to share a transverse arching and slight median indentation at the sagittal line. Each anterior band of the pleurae composing the pleural regions of the pygidium of *P. borealis* carries a conspicuous ornamentation comprising up to three distinct, subparallel ridges (somewhat resembling terrace-lines) that begin transversely at the fulcrum and then curve strongly back posterolaterally, terminating at the border furrow. A similar form of ornamentation is seen on the pygidium of *P. parabola* (see Kielan 1960 : 73) and in both forms it is accompanied by numerous closely spaced punctae, particularly on the abaxial portions of the pleural fields. Another interesting feature common to both *P. parabola* and *P. borealis* is the presence in the axial furrows of the cranidium of two pairs of small pits, structures first described by Kielan (1960 : 72), who termed them anterior and posterior pits, and later confirmed in Welsh Ashgill material by Whittington (1966 : 79). Similar pits have not yet been seen in *P. matutina* but the corresponding part of the exoskeleton is incompletely preserved.

The above notes suggest there is some justification for retaining *P. borealis* in *Phillipsinella,* whilst the Turkish specimens do not exhibit sufficient features to warrant placing them in a separate genus.

Tripp (1962 : 9) stated that *P. borealis* appeared to be referable to *Kirkdomina* as the cranidium agreed in all essential features with that of the type species *K. williamsi* Tripp (1962 : 9, pl. 2, figs. 4, 5) from the Confinis Flags (Porterfield Stage) of the Girvan District, Scotland. At the time of its introduction *K. williamsi* was known only from a cephalon and a cranidium and was placed in the Family Styginidae, but subsequently Tripp (1967 : 48, pl. 1, figs. 27, 28) described from the Stinchar Limestone a cranidium and an isolated pygidium of styginid type that were assumed to belong to the same species. Whether or not the latter pygidium is correctly attributed to *K. williamsi,* Tripp's assertion (1962 : 10) that the pygidium of *P. borealis* is of styginid type seems to me dubious, and Kummerow's species has more features in common with the Phillipsinellidae than with the Styginidae, which are in turn regarded by Whittington (1963 : 83) as synonymous with the Scutelluidae. The supposed relationship of *P. borealis* to *K. williamsi* on the basis of the cranidium may be more securely founded, but is not yet proven.

Family **LICHIDAE** Hawle & Corda, 1847

Genus ***METOPOLICHAS*** Gürich, 1901

TYPE SPECIES. *Metopias hübneri* Eichwald, 1842.

Metopolichas sp.

(Pl. 5, figs. 1, 7, 8, 12, 15; Pl. 6, figs. 1, 5, 10, 15)

FIGURED SPECIMENS. BM. It.7905 (Pl. 5, fig. 1), It.7929 (Pl. 5, figs. 7, 12, 15), It.7930 (Pl. 5, fig. 8), It.7932 (Pl. 6, figs. 1, 5), It.7938 (Pl. 6, fig. 10), It.7942 (Pl. 6, fig. 15).

LOCALITY AND HORIZON. B.651 at the Sobova Valley section, in the limestone member of the Sobova Formation.

DESCRIPTION. A single fragmentary cranidium shows the outline of the median glabellar lobe to be narrowest immediately behind its centre. Thence the anterior half of the median lobe becomes broader anteriorly, its sides bounded by longitudinal furrows which are deepest here, diverging forwards at slightly less than a right-angle, but which become slightly shallower posteriorly and curve through almost 180 degrees around the elliptical bicomposite lateral lobes. Opposite the posterior half of the bicomposite lobes, the median glabellar lobe is narrow and slightly depressed, but behind them it broadens and becomes slightly more convex until truncated by the deep, transversely straight occipital furrow. The hindmost portion of the median lobe is not sharply defined laterally, and the longitudinal furrows there are represented only by a pair of shallow depressions, the left one of which is slightly the shallower.

The hypostoma is slightly broader than long, its posterior margin indented by a conspicuous, rounded median notch. The relatively large, parallel-sided median body occupies about five-eighths of the overall length and slightly more than half the total breadth, and is completely circumscribed by a deep, broad furrow; its posterior margin is transversely straight but the anterior margin is broadly rounded. The median body is divided into two unequal lobes, the posterior of which is much the smaller, by a median furrow that is deep and broad (*exsag.*) abaxially but obsolete medially, so that it forms in effect a pair of furrows that run inwards and diagonally backwards. Consequently the posterior lobe narrows (*sag.*) medially but abaxially has the appearance of a pair of sub-triangular lobes not unlike basal glabellar lobes. The anterior lobe occupies almost two-thirds of the length of the median body and is transversely oval in outline. The anterior wings are small, sited opposite the centre of the anterior lobe and continuous with the narrow (*sag.*) anterior border. Immediately behind them is a pair of small lateral notches, to the rear of which the hypostomal outline broadens rapidly to attain its maximum opposite the posterior lobe before narrowing more gradually to the bifurcated posterior margin. The surface of the posterior wings is ornamented laterally with anastomosing ridges that become weaker and pass into lines of small tubercles towards the median notch, whilst that of the median body, excluding furrows, is covered with closely grouped punctae (see Pl. 6, fig. 15).

The pygidium is represented by only a single fragment (Pl. 5, fig. 8) showing the incomplete left half of the doublure and part of the external mould of the dorsal exoskeleton. Two pairs of large pleural spines are evident, their free points directed almost posteriorly; the pygidial margin at the sagittal line is not preserved but there is no indication of a third pair of pleural spines. The outer surface of the doublure is covered with conspicuous anastomosing terrace-lines that follow a course subparallel to the pygidial margin, including spines. Risk of breakage has not permitted the use of latex to make a cast of what remains of the dorsal exoskeleton, but a plasticine cast shows the tip of the axis to be swollen, passing posteriorly into a low ridge, whilst the pleural region has two pairs of pleurae that carry deep pleural furrows and are separated by equally deep interpleural furrows. The surface of the exoskeleton is covered with coarse, closely grouped tubercles, a characteristic form of lichid ornamentation shown also on broken fragments of the cranidium (see Pl. 5, fig. 1).

DIMENSIONS (in mm, IM = internal mould, EM = external mould).

Cranidium		It.7932	
Median length of glabella		6·2 estd (IM)	
Max. breadth of median glabellar lobe		4·2 (IM)	
Min. breadth of median glabellar lobe		1·4 (IM)	
Estd basal breadth of median glabellar lobe		2·2 (IM)	
Hypostoma	It.7929	It.7938	It.7942
Overall length	6·8 (IM)	6·5 estd (EM)	5·7 (EM)
Median length	5·5 (IM)	5·3 (IM)	4·8 (EM)
Overall breadth	7·0 (EM)	6·6 estd (EM)	5·8 estd (EM)
Length of middle body	4·2 (IM)	4·1 (IM)	3·7 (EM)
Breadth of middle body	4·3 (EM)	3·9 (EM)	–

DISCUSSION. The systematic position of such incomplete material is not certain but the hypostoma matches best that of *Metopolichas*, and the fragmentary cranidium and pygidium do not disagree with this evidence. Tripp (1957 : 113) pointed out that although the hypostoma of the type species *M. huebneri* (Eichwald), from the Middle Ordovician of Estonia, is not known, the structure has been described for six other species customarily ascribed to the genus. The hypostoma of the Sobova species does not agree with any previously described, and additional material would probably necessitate the erection of a new name. In some respects it resembles the hypostoma of *M. verrucosus* (Eichwald) as figured from the Asaphus Limestone of Öland, Sweden, by Warburg (1939 : pl. 3, figs. 3, 4) but the Turkish specimens have a longer, more nearly parallel-sided median body on which the anterior lobe is larger and more tumid ; the lateral border is narrower frontally ; and the posterior wings do not project so far laterally.

Although Tripp (*in* Moore, 1959 : O 496) stated that in *Metopolichas* the longitudinal furrows do not extend beyond (i.e. longitudinally behind) the bicomposite lateral lobes, in certain of the species attributed by him to the genus (Tripp 1958 : 575) there is evidence that the furrows extend, in an attenuated form, to the occipital furrow. Tripp (1957 : 113) had earlier noted that in the closely related genus *Lichas* (s.s.) some species ' are equivocal in their cranidial features ' and it seems likely that *Metopolichas* behaves in a similarly variable manner. Detailed comparison of the Sobova cranidium is not possible but it bears some resemblance to that of *M. erici* (Warburg 1939 : 34, pl. 5, figs. 1, 2), described from the Asaphus Limestone of Öland, Sweden, and said to occur also in Stage B_{2b} of the East Baltic region. The Swedish species may be distinguished by the position of the bicomposite glabellar lobes, which are set slightly farther forwards, whilst the base of the median glabellar lobe is relatively narrower (though bounded laterally by similar shallow depressions) and the frontal glabellar lobe projects forwards more strongly.

Family **CYCLOPYGIDAE** Raymond, 1925

Genus ***PRICYCLOPYGE*** R. & E. Richter, 1954

Type species. *Aeglina prisca* Barrande, 1872, from the Šárka Beds, Llanvirn Series of Bohemia, by original designation. Nowadays *Pricyclopyge prisca* is regarded as a subjective synonym of *P. binodosa* (Salter, 1859) – see later.

Pricyclopyge superciliata sp. nov.

(Pl. 6, figs. 2, 4, 6, 8, 9, 14)

Diagnosis. *Pricyclopyge* with occipital ring and unfurrowed glabella confluent, their combined length just less than their maximum breadth; combined outline expands forwards to maximum just in front of centre. Frontal glabellar lobe broadly rounded in plan. Anterior halves of fixigenae narrow, band-like; posterior halves small, triangular.

Holotype. BM. It.7933 (Pl. 6, figs. 2, 6, 8).

Paratypes. BM. It.7935 (Pl. 6, fig. 4), It.7937 (Pl. 6, fig. 9), It.7941 (Pl. 6, fig. 14).

Locality and horizon. The species is known only from locality C.429, 1·5 km east of the village of Kızılca, 17 km northwest of Seydişehir. The locality is in limestones correlated broadly with the limestone member of the Sobova Formation, but see discussion of age later.

Description. Only a few cranidia and fragmentary librigenae are available. The largest cranidium is slightly wider than long, composed largely of the confluent glabella and occipital ring, with very small fixigenae. The outline of combined glabella and occipital ring is narrowest posteriorly but expands by about one-third to attain its maximum breadth just in front of centre; from there it narrows more gradually, so that the outline of the frontal glabellar lobe is bluntly rounded. In lateral view the dorsal surface of the glabella declines forwards only gently for just over two-thirds of its length but then turns sharply down and slightly back (see Pl. 6, fig. 8). Neither occipital furrow nor glabellar furrows are clearly developed, though their presence is suggested by faint depressions. There is also evidence that the occipital ring was divided into two unequal bands, the anterior twice the breadth (*sag.*) of the posterior, by a pair of short (*tr.*) intra-occipital furrows that are preserved on the internal mould of the larger cranidium (see Pl. 6, fig. 6). The fixigenae are of minimal size and extend forwards just over three-quarters of the length of the cranidium. Posteriorly they form small sub-triangular areas with the posterior branches of the facial suture curving backwards strongly; anteriorly they are continuous with the palpebral lobes, which form a pair of narrow strips that become slightly narrower (*tr.*) forwards alongside the narrow axial furrows. Two fragmentary librigenae are illustrated. One of these (Pl. 6, fig. 4) retains part of the visual surface of the eye which, although incomplete, exhibits at least 45 vertical rows of small lenses, with a minimum of 27 lenses present per row in the median portion. The lenses are hexagonally arranged and decrease in size from top to bottom of the eye surface. Part of a right librigena (Pl. 6, fig. 9) has up to 33 lenses in each vertical row and retains part of the doublure with several terrace-lines.

The remainder of the exoskeleton is not known.

DIMENSIONS (in mm, IM = internal mould, EM = external mould).

	It.7933	It.7941
Length of cranidium	5·2 (IM)	3·2 (IM)
Median breadth of cranidium	5·8 (IM)	4·3 estd
Max. breadth of glabella	4·8 (IM)	3·5 estd (IM)
Basal breadth of glabella	3·6 (EM)	–

DISCUSSION. The close resemblance of the type species *Pricyclopyge prisca* (Barrande) to the earlier-described *P. binodosa* (Salter) was noted by Whittard (1961 : 175) who nevertheless retained them as separate taxa. Subsequently, however, Marek (1961 : 30 *et seq.*) regarded them as subjectively synonymous, but distinguished two subspecies within Salter's species, namely *P. binodosa binodosa* (Salter) and *P. binodosa longicephala* (Klouček). In the Anglo-Welsh area *P. binodosa binodosa* ranges through the Upper Arenig and Lower Llanvirn Series, particularly the latter, but in Bohemia it is recorded only from the Šárka Beds, of Llanvirn age. The ample illustrations provided by Whittard (1961 : 172, pl. 23, figs. 7–20) and Marek (1961 : 31, pl. 1, fig. 20 ; pl. 2, figs. 1–11) show that although the glabellar outline of *P. binodosa binodosa* is generally similar to that of the new Turkish species, it is slightly shorter and the posterior halves of the axial furrows are more divergent forwards, whilst the combined palpebral lobes and fixigenae are narrower. The glabella of *P. binodosa longicephala* (Klouček) from the Dobrotivá Beds, Llandeilo Series, of Bohemia (see Marek, 1961 : 34, pl. 1, fig. 21 ; pl. 2, fig. 12) resembles *P. superciliata* more closely but the maximum breadth is attained farther forwards ; the eye extends farther back, so that the posterior halves of the fixigenae are smaller ; there is even less evidence of occipital and glabellar furrows ; and the eyes appear to have a large number of smaller lenses, though no detailed comparison is possible.

Cyclopyge latifrons Tjernvik (1956 : 259, pl. 10, figs. 9–11, text-fig. 42A), based on a single cranidium from the Grey Ceratopyge Limestone (Tremadoc Series) of Öland, has been referred to *Pricyclopyge* by Marek (1961 : 31). *P. latifrons* has a deeper, broader and shorter cranidium than the new species, the axial furrows are less conspicuously developed, and the combined fixigenae and palpebral lobes are smaller and narrower. *Cyclopyge gallica* Tjernvik (1956 : 260, pl. 10, figs. 12–16), so named because of its supposed similarity to an unnamed species of Lower Arenig age in the Montagne Noire of southern France, was based on type material from the Lower Planilimbata Limestone of Sweden. The glabella is proportionately shorter than that of *P. superciliata*, its outline more rounded frontally and less constricted basally, whilst the axial furrows are less well developed, the palpebral lobes are smaller and narrower, and the posterior halves of the fixigenae are even smaller.

The only undoubted evidence of cyclopygids in the Sobova Formation so far available is from locality C.429, but a small pygidium It.7934 (Pl. 6, fig. 3) from the limestone member at B.651 is provisionally referred to this family, though its systematic position is in doubt. Semielliptical in outline, this specimen has an axis that occupies about half the maximum breadth and two-thirds the median length, and is bounded by straight axial furrows that converge at about 40 degrees to the small blunt tip. The axial furrows are shallow and the axis stands scarcely higher than the pleural fields which are only gently convex and grade into a broad border that narrows a little anterolaterally. The axis has one large axial ring whilst the pleural fields shows traces of one pair of interpleural furrows, with one pair of pleural furrows deepening abaxially. These furrows are apparent on the internal mould, but a small fragment of the exoskeleton suggests that most of the external surface was smooth. The pygidium is not so straight-sided posterolaterally as that of a typical *Pricyclopyge*, though the length and shape of the axis and the breadth of the border are not inappropriate. The form of the axis and the essentially smooth pleural fields might also be compared with *Microparia* (see Marek 1961 : 36 *et seq.*), though the pygidium of the latter is generally longer and more rounded in plan.

Family **SCUTELLUIDAE** R. & E. Richter, 1955

Genus ***PROTOSTYGINA*** Prantl & Přibyl, 1948

TYPE SPECIES. *Illaenus bohemicus* Barrande, 1872.

Protostygina sp.

(Pl. 7, figs. 1, 3, 5, 10)

FIGURED SPECIMEN. BM. It.7943.

LOCALITY AND HORIZON. B.651 at the Sobova Valley, in the limestone member of the Sobova Formation.

DIMENSIONS (IM = internal mould, EM = external mould). Maximum breadth of pygidium = 20·0 mm estd (IM); median length = 8·0 mm (EM); frontal breadth of axis = 3·5 mm estd (EM).

DESCRIPTION. A large distinctive pygidium is transversely elliptical in outline, notably broader than long, with a median length three-sevenths of the maximum breadth. The front of the pygidium forms a straight, transverse line for most of its length (*tr.*) but ends in bluntly truncated articulating facets. The dorsal surface is flattened medially and arches gently down distally. The axis is of low convexity frontally, where it has a breadth one-fifth that of the pygidium ; it is bounded by straight axial furrows that converge at about 35 degrees and quickly die out, so that the tip of the axis merges with the smooth pleural regions. Frontally a single axial ring is defined by a shallow, transversely straight ring furrow ; the presence of a further five axial rings is indicated by the drawing together of the low ridges composing the ornamentation rather than by definite ring furrows. The remaining outer surface of the dorsal exoskeleton is ornamented for the most part with fine, closely spaced terrace-lines ; on the pleural regions these are arranged subparallel to the posterolateral margins, but they change direction at the axial furrows and run in curves across the axis, moderately convex forwards near the axial tip but becoming progressively straighter frontally. The external mould of the inner surface of the dorsal exoskeleton is pitted, indicating fine granular ornamentation (see Pl. 7, fig. 3). The doublure is large, its adaxial boundary forming a smooth curve of slightly greater radius than the pygidial margin and extending from the front of the pygidium at the inner ends of the articulating facets. Its ventral surface is ornamented with the fine terrace-lines which curve abaxially at the points where the anterolateral facets turn downwards (see Pl. 7, fig. 10). It is not known whether the curvature of the inner margin of the doublure is unbroken behind the tip of the axis, but this is probably the case.

Discussion. Barrande's holotype of *Illaenus bohemicus* (1872 : 68, pl. 11, fig. 12), the type species of *Protostygina*, is an almost complete but damaged dorsal exoskeleton which lacks the greater part of the pygidial margin. The specimen, which came from the Šárka Formation, Llanvirn Series, of Osek, Bohemia, was noted briefly by Raymond (1916 : 12) who considered it not to be an illaenid. Additional, better-preserved topotype material has since been described by Klouček (1916 : 10) and Prantl & Přibyl (1948 : 12, pl. 2, fig. 2 ; pl. 3, fig. 1). These specimens, particularly the last cited, suggest that the pygidial proportions, size of axis and, probably, the form of the doublure are comparable in the Turkish specimen. The latter differs in having the axial and ring furrows (the latter of similar number) still less well defined ; the doublure is slightly broader (*exsag.*), and the outline is truncated anterolaterally by facets that run more strongly back abaxially.

Family **ILLAENIDAE** Hawle & Corda, 1847

Subfamily **ILLAENINAE** Hawle & Corda, 1847

Genus ***ILLAENUS*** Dalman, 1827

Type species. *Entomostracites crassicauda* Wahlenberg, 1821.

Illaenus cf. ***herculeus*** Gortani

(Pl. 6, figs. 7, 11, 13, 16 ; Pl. 7, figs. 6–8, 11, 13, 14)

1934 *Illaenus Esmarki* Schlotheim sp., Gortani, p. 83, pl. 18, figs. 7a–c.
1934 *Illaenus herculeus* Gortani, p. 85, pl. 19, figs. 1a–d.

FIGURED SPECIMENS. BM. It.7936 (Pl. 6, figs. 7, 11, 16), It.7940 (Pl. 6, fig. 13), It.7945 (Pl. 7, figs. 6, 7, 13), It.7946 (Pl. 7, figs. 8, 11, 14).

LOCALITY AND HORIZON. B.651 at the Sobova Valley, in the limestone member of the Sobova Formation.

DESCRIPTION. *Illaenus herculeus* was founded by Gortani on a single large incomplete cephalon and thorax from the Karakorum Himalayas, in rocks of ' level d (red beds) ' where it was said to be associated with *Nileus armadillo* Dalman, *Illaenus esmarki* (Schlotheim) and *Panderia raniceps* (Gortani). The specimen described as *I. esmarki* is a cephalon with breadth two-thirds that of *I. herculeus*, from which it does not appear to differ significantly. The axial furrows of ' *I. esmarki* ' are slightly concave abaxially on the illustration and extend forwards a little farther than those of *I. herculeus* ; in this respect it much resembles the Turkish material, especially Pl. 6, fig. 16, a cranidium in which the axial furrows are deeper and extend farther forwards on the internal mould than on the corresponding outer surface of the exoskeleton. The ornamentation of raised lines forming a Bertillon pattern matches that shown by Gortani's illustrations.

Neither hypostoma nor pygidium of *I. herculeus* and ' *I. esmarki* ' was available to Gortani, so it is not possible to state whether the Sobova Formation pygidia noted below belong here, though it seems unlikely. A single associated hypostoma (Pl. 6, fig. 13) illustrated as an internal mould with median length 3·8 mm is of the type described for *Illaenus* (s.s.) as exemplified by *I. sarsi* Jaanusson (1954 : pl. 2, figs. 1, 2 ; Fig. 9A). Like *I. sarsi*, the Sobova hypostoma has a transversely straight anterior margin with a broad (*sag.*) anterior border passing into large, quadrate anterior wings; a subelliptical middle body divided into two unequal lobes ; and a narrow (*sag.*) unbroken posterior border. The Turkish hypostoma differs only in detail, having a slightly longer, less elliptical middle body and anterior wings that are both narrower (*exsag.*) and longer (*tr.*).

DIMENSIONS (in mm, IM = internal mould, EM = external mould).

	It.7936	It.7945	It.7946
Median length of cranidium	5·0 (EM)	4·0 (IM)	13·5 estd (EM)
Frontal breadth of cranidium	6·2 (EM)	4·6 (IM)	18·0 estd (IM)
Basal breadth of glabella	3·2 (EM)	2·6 (EM)	9·3 estd (EM)
Distance across palpebral lobes	–	5·4 estd (EM)	18·6 estd (EM)

Illaenid genus and species undetermined

(Pl. 6, fig. 12 ; Pl. 7, fig. 12)

FIGURED SPECIMENS. BM. It.7939 (Pl. 6, fig. 12), It.7947 (Pl. 7, fig. 12).

LOCALITY AND HORIZON. B.651 at the Sobova Valley section, in the limestone member of the Sobova Formation.

DESCRIPTION. Two small pygidia are subsemicircular in outline with the anterior margin running slightly backwards abaxially from the axial furrows to well-rounded anterolateral angles. The axis is narrow, its frontal breadth about one-quarter that of the pygidium ; it is bounded by straight axial furrows that converge backwards gently and, although deep frontally, become shallower and die out about halfway to the posterior margin. The larger pygidium shows traces of three narrow (*sag.*) axial rings on the internal mould (Pl. 7, fig. 12), and the tip of the axis is not clearly defined ; the corresponding external mould lacks the axial rings and the axial tip is still less clear. The smaller pygidium (Pl. 6, fig. 12) has the axis better defined on the internal mould. Each specimen has a pair of narrow (*exsag.*) anterior half-ribs and a pair of small anterolateral facets, but the pleural regions are otherwise smooth on both outer surface and internal mould.

DIMENSIONS (in mm, IM = internal mould, EM = external mould).

	It.7939	It.7947
Max. breadth of pygidium	4·0 estd (IM)	8·0 (IM)
Median length of pygidium	2·3 (IM)	4·7 (IM)
Frontal breadth of axis	1·0 (IM)	1·9 (IM)
Length of axis	1·2 (IM)	2·3 (IM)

DISCUSSION. Although not generically determinable with certainty, the pygidia may be compared with that of *Dysplanus* Burmeister, 1843. Illustrations of the type species, *D. centrotus* (Dalman), first described from the Expansus Limestone of Sweden, have been given by both Holm (1882 : pl. 4, figs. 2, 10) and Jaanusson (1957 : pl. 1, figs. 7, 8 ; *in* Moore 1959 : Fig. 283, 7d), and appear to agree essentially with the specimens now considered. In particular the original of Holm's pl. 4, fig. 10 shows axial rings of similar form and size, though the number visible is five instead of three ; in addition the tip of the axis is even less well defined and the pygidial outline is slightly longer and more rounded.

The Sobova specimens bear a general resemblance to two pygidia from the Lower Ordovician of the Karakorum Himalayas figured by Gortani as *Illaenus Dalmani* Holm (Gortani 1934 : 87, pl. 19, figs. 2a–c) and *Illaenus spitiensis* Reed (Gortani 1934 : 88, pl. 19, figs. 3a, b). The first of the two latter is proportionately a little longer than It.7947, and the axial furrows are slightly more convergent, but the pleural regions are similar. The other Himalayan specimen, the smaller of the two, has a better defined, more strongly tapered axis than the smaller Turkish specimen, and is also proportionately longer, but again the pleural regions are broadly similar. Both Gortani's specimens came from the same locality and horizon and may well represent a single species. Neither agrees in detail with *Illaenus spitiensis* Reed (1912 : 95, pl. 14, figs. 4–14) from the Central Himalayas, a species in which the pygidium has an almost subcircular outline, a conspicuous pair of pleural furrows anterolaterally and a short triangular axis. On the other hand, *Illaenus dalmani*, first described by Volborth (1863 : 13, pl. 2, figs. 7–13) as *I. crassicauda* var. *Dalmani*, and later redescribed by Holm (1886 : 93, pl. 1, figs. 7–14) is younger than the Turkish specimens and is distinct from both of them and, probably, the Himalayan material.

Subfamily **PANDERIINAE** Bruton, 1968

(nom. corr. herein *ex* **PANDERINAE** Bruton, 1968)

Genus ***PANDERIA*** Volborth, 1863

TYPE SPECIES. *Panderia triquetra* Volborth, 1863.

Panderia monodi sp. nov.

(Pl. 9, figs. 2–4, 7–9 ; Pl. 10, figs. 2, 5, 6–9)

DIAGNOSIS. Cranidium strongly convex and steeply declined anteriorly. Glabella defined only posteriorly by deep axial furrows that extend forwards about half length of cranidium. Eyes large, with palpebral furrows developed on internal mould but almost effaced on surface of exoskeleton. Anterior branches of facial suture straight, subparallel, turning adaxially only upon reaching anterior margin. Small anterior border and anterior border furrow may be present. Median tubercle sited posteriorly on glabella. Pygidium sub-semielliptical in plan, strongly convex. Narrow axis with straight sides defined only frontally on outer surface of exoskeleton ; internal mould has better-defined, broad axial furrows almost to tip of axis, together with five ring furrows and, parallel to margin, a ' border furrow ' that is not visible on the outer surface and may coincide with inner margin of doublure.

HOLOTYPE. BM. It.7958 (Pl. 9, figs. 4, 8, 9).

PARATYPES. BM. It.7957 (Pl. 9, figs. 2, 3, 7), It.7962 (Pl. 10, figs. 2, 5, 6), It.7963 (Pl. 10, figs. 7–9).

LOCALITY AND HORIZON. Sobova Valley, locality B.651, in the limestone member of the Sobova Formation.

DESCRIPTION. The exoskeleton is known only from isolated cranidia and pygidia. The cranidium is one and a half times as broad as long in dorsal view, transversely convex, with front strongly arched downwards and slightly backwards. Only the posterior half of the glabella is defined laterally, by axial furrows that are well developed on both outer surface of the exoskeleton and the corresponding internal mould (see Pl. 9, figs. 8, 9) and terminate behind a line joining the anterior ends of the palpebral lobes. No occipital furrow is visible on internal mould or external surface. The semielliptical palpebral lobes are positioned behind centre with respect to the cranidium ; their dorsal surface appears smooth but the internal mould of the largest cranidia shows each lobe to be narrow, delimited by a conspicuous palpebral furrow that dies out both anteriorly and posteriorly where it merges with the branches of the facial suture. The latter has the anterior branches straight and parallel as far as the margin of the cranidium, where they turn inwards through a right-angle and meet frontally in a gentle curve. The posterior branches curve backwards strongly to cut the posterior margin longitudinally in line with the palpebral lobes. The posterior halves of the fixigenae thus delimited form very small triangles, separated from the posterior border by a posterior border furrow that is markedly shallow immediately outside the axial furrows. The glabella has no trace of glabellar furrows and is undefined anteriorly, where the front of the cranidium has a narrow (*sag.*), slightly upturned anterior border, bounded by a broad (*sag.*), shallow anterior border furrow. The above description applies especially to the holotype, a presumably mature cranidium which differs in some respects from a small paratype cranidium (Pl. 10, figs. 7–9) that is slightly distorted. In particular the unfurrowed area between the palpebral lobes and the frontal margin is proportionately longer, the anterior border and anterior border furrow are narrower (*sag.*), and the palpebral furrows are less well defined on the internal mould. There is insufficient evidence to suggest that such differences are more than intraspecific, reflecting different stages of ontogeny. The smallest cranidium has a small median tubercle on the glabella opposite the centre of the palpebral lobes, but on a larger specimen the corresponding structure is positioned farther back, opposite the posterior end of the palpebral lobes. Possibly the position of the tubercle changed during ontogeny.

The remainder of the cephalon and the thorax are unknown.

The pygidium, represented by one large and one small example, is almost semicircular in plan, moderately convex both longitudinally and transversely ; the anterior margin, excluding articulating half-ring, is transversely straight medially but then runs slightly backwards abaxially and meets the lateral margins almost at right-angles. The axis is nearly an isosceles triangle in outline, with straight sides converging backwards at about 30 degrees to a blunt tip. The front of the axis occupies almost one-third of the anterior breadth of the pygidium. The axial furrows are conspicuous, very broad on the internal mould but only moderately deep, with the inner margins less steep than the outer margins. As far as may be judged from the internal mould, the axis is fairly well segmented, with the first axial ring complete and well defined ; the remaining rings, of which there are traces of at least four, are apparently less well-defined medially than laterally. The surface of the pleural fields declines gently abaxially as far as a well-defined ‘ border furrow ’ which runs parallel to the margins and about one-fifth of the distance from each lateral margin to the sagittal line. The term ‘ border furrow ’ is used here with some reservations as to its true nature. The corresponding portion of the dorsal surface of the exoskeleton of the larger pygidium has not been found but is seen to be smooth in the smaller specimen. It may be that the ‘ border furrow ’ of the internal mould coincides with the inner margin of the doublure, though the latter has not yet been seen. The ‘ border furrow ’ marks a change in slope of the surface of the pleural region which declines thence more steeply to the pygidial margin. The foremost part of each pleural region carries an anterior half-rib which is separated by a broad (*exsag.*) furrow and expands anterolaterally to a pair of facets. On the internal mould, at least, the facets mark the anterior limit of the ‘ border furrow ’ described above. The pleural fields show traces of segmentation but the number of ribs present cannot be distinguished with certainty.

DIMENSIONS (in mm ; IM = internal mould, EM = external mould).

	It.7957	It.7958	It.7962	It.7963
Frontal breadth of cranidium	–	7·2 estd (IM)	–	4·3 (EM)
Maximum breadth of glabella	10·4 estd (IM)	6·2 (IM)	–	4·5 estd (EM)
Distance across palpebral lobes	15·6 estd (EM)	9·6 (IM)	–	6·6 (EM)
Posterior breadth of combined glabella and occipital ring	8·4 estd (EM)	5·1 (IM)	–	3·0 (IM)
Position of median tubercle	Slightly in front of transverse line through posterior ends of palpebral lobes	Not preserved	–	Opposite centre of palpebral lobes
Distance from median tubercle to posterior cephalic margin	5·5 (EM)	–	–	2·9 estd (EM)
Maximum breadth of pygidium	–	–	15·0 (IM)	–
Median length of pygidium (excluding articulating half-ring)	–	–	9·0 estd (IM)	–
Frontal breadth of axis	–	–	4·5 (IM)	–

DISCUSSION. Bruton (1968) has reviewed the various species of *Panderia* present in Scandinavia and the Baltic region, where the genus ranges through much of the Ordovician. None of these species seems likely to be confused with *Panderia monodi* which may, in some respects, be compared with the genus *Ottenbyaspis*, founded by Bruton (1968 : 29, pl. 12, figs. 4, 7–12) on *Illaenus oriens* Moberg & Segerberg, 1906, originally from the Tremadoc Series, *Apatokephalus serratus* Zone, of Öland and redescribed by Tjernvik (1956 : 217, pl. 3, figs. 12–18) who assigned the species to *Symphysurina* ? There is clearly a considerable resemblance between *Panderia* and *Ottenbyaspis*, and Dr Valdar Jaanusson, who has been studying these genera, kindly informs me (personal communication, 1972) that in his opinion the two grade into one another and that, *inter alia*, the position of the median glabellar tubercle – according to him a constant feature within a species – indicates *Panderia* rather than *Ottenbyaspis* in the present instance. On one of the paratypes of *P. monodi* the median tubercle is sited opposite the posterior ends of the palpebral lobes, and in another paratype is set farther forwards, opposite the centre of the palpebral lobes, but the material is insufficient to demonstrate fully the variability of this feature. *O. oriens* differs from *P. monodi* in the following respects : the cranidium is of lower transverse convexity ; the axial furrows become shallower anteriorly ; the fixigenae are slightly wider ; the front of the cranidium is proportionately wider ; the pygidium is relatively shorter, its border is wider, the pleural fields are smaller and the axis is larger and better segmented on the internal mould.

The cranidium of *Ottenbyaspis perseverans* (Tjernvik 1956 : 218, pl. 3, figs. 19–22), from the Arenig Series of Västergötland, has the anterior border closely similar to that of *P. monodi* but may be distinguished by the lesser transverse convexity of the glabella, the divergence forwards of the anterior branches of the facial suture, and the slightly less well-developed axial furrows. The pygidium of *O. perseverans* is proportionately shorter even than that of *O. oriens* and the ' border ' (see description above) is notably wider than that of *P. monodi.*

Detailed comparison with *Illaenus* (*Panderia*) *raniceps* Gortani (1934 : 90, pl. 19, figs. 5a–d) is not practicable until the original material is redescribed, though it would appear that the eyes are set farther forward than those of the new species. *I.* (*P.*) *raniceps* was described from the Ordovician of the Karakorum where it was said to occur with *Nileus armadillo* (Dalman), *Illaenus esmarki* (Schlotheim) and *I. herculeus* Gortani ; its age may thus be similar to that of the present material.

Family **NILEIDAE** Angelin, 1854

Genus ***NILEUS*** Dalman, 1827

TYPE SPECIES. *Asaphus* (*Nileus*) *armadillo* Dalman, 1827.

Nileus sp.

(Pl. 8, figs. 2, 3, 8–10, 14 ; Pl. 11, fig. 7)

FIGURED SPECIMENS. BM. It.7949 (Pl. 8, figs. 2, 3, 10), It.7952 (Pl. 8, figs. 8, 9, 14), It.7969 (Pl. 11, fig. 7).

LOCALITY AND HORIZON. Found as yet only at locality C.429, 1·5 km east of Kızılca, in pink, crystalline limestone of the Sobova Formation.

DESCRIPTION. *Nileus* is represented in the present small sample by only two incomplete cranidia and one hypostoma. The glabella and occipital ring together constitute a single, almost continuous structure which is subparallel-sided for two-thirds its length but then, particularly on the larger cranidium, expands immediately in front of the palpebral lobes to form a frontal glabellar lobe that is broadly rounded in plan. The small occipital ring is broadest (*sag.*) medially, marked by a shallow occipital furrow that is visible only on the internal mould. The palpebral lobes are sited slightly behind centre with reference to the combined glabella and occipital ring, and their flat dorsal surfaces are steeply declined forwards (see Pl. 8, fig. 8) ; in plan they appear elongated and semielliptical, and their overall breadth is rather more than one and a half times the adjacent glabellar breadth. A small median tubercle is sited on the glabella a little behind the line of the mid-point of the palpebral lobes.

The hypostoma has a length almost five-sixths of the overall breadth and the middle body is notably large, its maximum breadth about two-thirds that of the whole. The large, convex anterior lobe is subcircular in outline, transversely truncated frontally but bounded posteriorly by a conspicuous median furrow, the abaxial portions of which are deep and curve adaxially backwards at first, becoming almost obsolete as they flex inwards to meet medially. The posterior lobe is crescentic in outline and ends in a pair of conspicuous, swollen maculae ; its posterior boundary becomes indistinct towards the axial line, where it merges with the edge of a shallow, rounded median notch that indents the posterior margin of the hypostoma. The posterior wings are of even breadth and extend forwards to within a short distance of the anterior border, so that the anterior wings, although not preserved, must have been very small. Traces of a few closely grouped terrace-lines persist on some marginal areas of the anterior lobe of the middle body.

DIMENSIONS (in mm).

	It.7949	It.7952
Frontal breadth of glabella	10·4 estd	–
Posterior breadth of glabella	8·4 estd	5·5
Median length of cranidium	10·8 estd	–
Distance across palpebral lobes	12·2 estd	8·9 estd

DISCUSSION. *Nileus* sp. has much in common with a number of species of early Ordovician age, and in particular the almost parallel-sided glabella resembles that of *Nileus limbatus* Brøgger (1882 : 62, pl. 12, fig. 7), described originally from the Tremadoc Series of Norway but since redescribed from Sweden where it ranges upwards into the Lower Arenig (Tjernvik, 1956 : 208). However, the frontal glabellar lobe of *N. limbatus* is less angular anterolaterally and more rounded frontally, and that of the present form may be better compared with *N. armadillo* (Dalman 1827) from the Expansus Limestone, Upper Arenig, of Östergötland, Sweden (Tjernvik, 1956 : 208, text-fig. 33D), though the upper of Tjernvik's drawings of the latter species shows the sides of the glabella more convex in outline. The hypostoma assigned to *Nileus* sp. is of the form characteristic for the genus, though unusually long, whilst the posterior wings are narrow and the anterior lobe of the middle body relatively large. In these respects it resembles *N. limbatus* rather than other species of *Nileus*.

The glabellar outline of *Nileus* sp. is also like that of *Platypeltoides serus* Tjernvik (1956 : 219, pl. 4, figs. 1, 2, text-fig. 35N) from the Lower Arenig of Sweden, but the latter's flattened anterior border, smaller eyes and larger posterior halves of the fixigenae are distinctive. The hypostoma from locality C.429 (see Pl. 11, fig. 7) also closely resembles that of *P. serus* (see Tjernvik 1956 : pl. 3, fig. 23) but has a more convex middle body, more distinct maculae and slightly longer, narrower posterior wings. Tjernvik (1956 : 219) noted the resemblance of the hypostoma of *Platypeltoides* to that of *Symphysurus*, which in turn resembles that of *Nileus*, but drew attention to the distinctive median process in the notched posterior margin of *Symphysurus*. Such a process is definitely absent from the Turkish specimen and was said to be lacking in *P. serus*, though there is a suggestion of it in Tjernvik's illustration. The hypostoma of the type species of *Platypeltoides*, *P. croftii* (Callaway 1877) from the Tremadoc of Shropshire, is imperfectly known but Lake's description (1942 : 314–15, text-fig. 5b) suggests that a median process is absent from the posterior indentation. Lindström (1901 : 62, pl. 5, figs. 13, 18) illustrated a median process on the type species of both *Nileus* and *Symphysurus* but stressed the variability found in the hypostoma of *Nileus armadillo*, and the latter has been figured more recently without a median process (Harrington *in* Moore 1959 : Fig. 42-17).

Genus ***SYMPHYSURUS*** Goldfuss, 1843

TYPE SPECIES. *Asaphus palpebrosus* Dalman, 1827.

Symphysurus pannuceus sp. nov.

(Pl. 8, figs. 1 ?, 4–7, 11–13 ; Pl. 9, figs. 5, 10–12 ; Pl. 10, fig. 4 ; Pl. 12, fig. 4)

DIAGNOSIS. Glabella and occipital ring continuous, strongly arched down anteriorly, almost as broad as long, outline slightly expanded frontally. Large palpebral lobes situated centrally. Pair of deep vincular notches near genal angles. Pygidium sub-semielliptical in plan with straight-sided axis two-thirds median length. Traces of four axial rings on internal mould. Pleural regions smooth except for anterior half-ribs.

HOLOTYPE. BM. It.7959 (Pl. 9, figs. 5, 10–12 ; Pl. 10, fig. 4).

PARATYPES. BM. It.7950 (Pl. 8, figs. 4–6), It.7951 (Pl. 8, fig. 7), It.7953 (Pl. 8, fig. 11), It.7954 (Pl. 8, fig. 12), It.7955 (Pl. 8, fig. 13), It.7976 (Pl. 12, fig. 4).

LOCALITY AND HORIZON. All the material available is from locality B.651 at the Sobova Valley section, in the limestone member of the Sobova Formation.

DESCRIPTION. The only complete cephalon is semielliptical in plan, strongly convex transversely and, especially, longitudinally. No occipital furrow is visible on internal or external mould, though this part of the exoskeleton is not well preserved, nor are there lateral glabellar furrows. The combined glabella and occipital ring appear especially convex in lateral view, strongly arched down frontally to overhang the anterior border. The glabella, surmounted by a small apical tubercle sited behind centre, is bounded by axial furrows which are shallowest medially, level with the eyes, but deepen to both back and, particularly, front where they form slot-like depressions immediately in front of which the front of the glabella broadens slightly (see Pl. 8, fig. 13). The palpebral lobes are semielliptical in plan, unfurrowed though slightly thickened posteriorly, their flat surfaces declined gently laterally but steeply forwards (see Pl. 8, fig. 5). The eyes are large, subcrescentic in plan, placed opposite the centre of the cephalon and with length about half that of the latter. The holochroal visual surfaces, though imperfectly preserved, are vertical and slightly convex ; below each is a narrow, raised band, bounded laterally by a furrow which indents the librigenal surface to form an eye platform and is notably conspicuous on the internal mould. The front of the glabella is separated by a narrow (*sag.*), shallow furrow from a diminutive, rim-like anterior border (see Pl. 9, figs. 5, 12), formed by the front of the conjoined librigenae. The border extends laterally until approximately level with the front of the eyes, at which point the librigenal margin is undercut by a pair of deep, sharply defined vincular notches which traverse the well-developed, convex doublure. When viewed laterally each librigena shows a concave indentation of the margin, coincident with the vincular notch (see Pl. 9, fig. 10). The margin near the genal angles is rounded, but the angles themselves are not completely preserved. The anterior branches of the facial suture cross the axial furrows immediately in front of the eyes, turn adaxially through a right-angle around the anterolateral extremities of the glabella, and then gradually traverse the anterior border furrow so as to meet frontally in a continuous, gentle curve just inside the low anterior border. The posterior branches are short, running in gently sigmoidal curves to cut the posterior margin just inside longitudinal lines through the edges of the palpebral lobes. The posterior halves of the fixigenae thus delimited are small, subtriangular, and slightly convex posteriorly, though there is no clearly defined posterior border. External moulds and fragments of exoskeleton show the surface of the glabella and occipital ring ornamented with low, anastomosing ridges arranged in a Bertillon pattern, subparallel to the lateral and frontal margins of the glabella. Similar ornamentation, though more weakly developed, occurs on part of the palpebral lobes and fixigenae but has not been found preserved on the librigenae.

The holotype possesses the only example of the complete thorax, comprising eight segments of the type characteristic for the genus. The convex axis stands high above the pleural regions and occupies anteriorly only slightly less than half the overall thoracic breadth, a proportion that decreases for the hindmost segments. It is bounded by well-defined, broad axial furrows in which each segment has a pair of large apodemes, positioned behind centre and visible on the internal mould (see Pl. 10, fig. 4). Each axial ring is transversely rectangular in plan, separated from the large articulating half-ring by an articulating furrow which is broad (*sag.*) on the internal mould but appears much narrower on the external surface. From the front of each pleura, at the axial furrow, a shallow pleural furrow runs gently backwards abaxially but is quickly truncated by a large, steeply declined articulating facet. The junction of facet and anterior pleural margin marks the location of an articulating process (see Pl. 12, fig. 4) which engages with a corresponding articulating socket on the preceding segment. The surface of each axial ring carries several curved, transverse ridges, like those of the glabella, which die out towards the furrows. Similar ridges occur, though not fully preserved, on the articulating facets and on the immediately adjacent portion of each pleura.

The pygidium is only moderately convex, both longitudinally and transversely, almost semielliptical in outline, with median length, excluding articulating half-ring, slightly more than half the maximum breadth. The front of the axis is separated from the half-ring by an articulating furrow which is gently curved forwards in plan, narrow (*sag.*) and shallow on the exterior of the exoskeleton but broad and deep on the internal mould. The axis has a frontal breadth one-third that of the pygidium and is bounded by straight axial furrows which are deepest frontally but become shallower as they converge to the blunt tip. Its length is just over two-thirds that of the pygidium and there is evidence of three or four poorly defined axial rings, separated by straight ring furrows which are shallowest medially. The frontal margin of the pygidium is transverse for only a short distance outside the axial furrows, and is then obliquely truncated by a pair of large articulating facets. The latter truncate also the anterior half-ribs and the single pair of deep pleural furrows. The surface of the facets carries closely grouped terrace-lines whilst similar though less crowded lines ornament the axis and the frontal portion of the pleural regions. In the case of the holotype the external surface of the abaxial portion of the pleural regions shows small, widely spaced punctae, but the impression of the corresponding internal surface indicates densely crowded, small granules. The holotype pygidium has the impression of a well-developed process below the abaxial end of the articulating facet (see Pl. 9, fig. 10) ; this corresponds to a vincular hook, as described by Harrington (*in* Moore 1959 : O 105, Fig. 78B), which functioned during enrollment by engaging with the cephalic vincular notch described earlier.

DIMENSIONS (in mm, EM = external mould, IM = internal mould).

	It.7950	It.7951	It.7953	It.7959
Max. breadth of cephalon	–	–	–	23·0* (IM)
Frontal breadth of glabella	15·0 (IM)	–	–	13·5 (IM)
Distance across palpebral lobes	23·7 (IM)	–	–	19·0* (IM)
Median length of cranidium	18·0 (IM)	–	–	13·7* (IM)
Max. breadth of pygidium	–	23·0* (IM)	20·7* (IM)	21·0* (IM)
Median length of pygidium	–	10·7* (IM)	10·5* (IM)	9·7 (IM)
Frontal breadth of axis	–	5·0 (IM)	6·4 (EM)	6·1 (IM)
Length of axis	–	7·0* (IM)	7·3 (EM)	7·0 (IM)

* Denotes estimated measurement.

DISCUSSION. Although *Symphysurus* is a frequently recorded genus, comprehensive modern illustrations of the Swedish type species *S. palpebrosus* (Dalman 1827) are not yet generally available, although Jaanusson (*in* Moore 1959 : Fig. 267, 8) has published a detailed drawing of the complete exoskeleton. Judging from this, *S. palpebrosus* bears a considerable resemblance to *S. pannuceus*, though the Swedish species differs in that the cephalon is probably less convex longitudinally and has the axial furrows more divergent forwards, whilst the pygidial axis is both narrower and shorter, and probably has fewer axial rings. According to V. Poulsen (1965 : 78) *S. palpebrosus* is characteristic of the highest Volkhovian and lowest Kundan Stages of Sweden (see Fig. 5) and is therefore of approximately similar age to the new species.

The cranidium of *Symphysurus pannuceus* is very like that of *S.* (*S.*) *dorsatus* V. Poulsen (1965 : 76, pl. 4, figs. 2–7) from the Skelbro Limestone, Arenig Series, of Bornholm, but the glabella appears even more tumid in both anterior and lateral views, and the axial furrows are less divergent forwards. The pygidium also closely resembles that of the Danish species and differs only in that the axis, which has a similar number of axial rings in both forms, is slightly broader, and the anterolateral angles of the pygidial outline are set farther forwards.

Also in the Sobova Valley, *Symphysurus blumenthali* Dean (1971 : 12) has been described from the highest part of the Seydişehir Formation and, whilst also of Arenig age, is slightly older than *S. pannuceus*. *S. blumenthali* may be distinguished from the new species by the much less convex glabella and by the proportionately shorter pygidium, with narrower, less well-defined axis.

The well-known Scandinavian species *Symphysurus angustatus* (Sars & Boeck, 1838), redescribed by Brøgger (1882 : 60, pl. 3, figs. 9, 10), Størmer (1940 : 143) and Tjernvik (1956 : 211, pl. 2, figs. 24, 25), has a slightly narrower, less convex glabella than *S. pannuceus*; the internal mould of the pygidium of *S. angustatus* is similar in outline, form of axis and number of axial rings, but the external surface is smoother. *S. angustatus* ranges from high Tremadoc to low Arenig Series in Scandinavia, and in the Mediterranean region has been described as being represented by the subspecies *S. angustatus sicardi* (Bergeron 1895 : 478; see also Thoral 1935 : 269), of supposed Tremadoc age but possibly from Arenig strata.

As far as the cephalon is concerned, another closely comparable species is *Symphysurus pater* (Holub 1912 : 2, pl. 1, figs. 2, 3; see also Prantl & Přibyl 1949 : 4, pl. 1, figs. 1, 2) from the Komárov Beds, Arenig Series, of Klabava, Bohemia, but the pygidium of the Czech trilobite is clearly distinct, being relatively shorter with the straight frontal margin turned less strongly back anterolaterally.

A single fragmentary hypostoma (It.7948, Pl. 8, fig. 1) from locality B.651, although too incomplete for certain identification, has the ornamentation of terrace-lines appropriate for *Symphysurus pannuceus* and is referred questionably to that species. The maximum length is estimated at just over three-fifths of the overall breadth, the posterior wings are broad and flat, and the median furrow is represented only by a pair of deep, broad (*exsag.*) notches that indent the sides of the median body immediately in front of a pair of poorly defined maculae.

Symphysurus sp.

(Pl. 9, fig. 1)

FIGURED SPECIMEN. BM. It.7956.

LOCALITY AND HORIZON. Locality C.429, 1·5 km east of Kızılca, in limestones of the Sobova Formation.

DESCRIPTION. A single incomplete pygidium has a maximum breadth and length of, respectively, 8·8 mm (estd) and 4·8 mm (estd), and is almost semielliptical in plan. The axis has a frontal breadth of 2·5 mm and on the outer surface of the exoskeleton its anterior half is bounded by straight axial furrows which are deep and broad frontally, converge only slightly, and die out just behind centre of the pygidium. On the internal mould the tip of the axis is indistinct. The surface of the axis, though slightly abraded, shows two axial rings, the first moderately defined, the second defined only laterally, but there is no clear evidence of further segmentation. The pleural regions are characteristic for the genus, moderately arched down and smooth for the most part, but with a large pair of articulating facets which truncate anterolaterally the anterior half-ribs. The last are bounded by pleural furrows which are deep and broad (*exsag.*) near the axial furrows but die out just outside the fulcra.

The specimen is inadequate for detailed comparison but has a narrower, less tapered axis than *Symphysurus pannuceus* from locality B.651, and is certainly distinct from that species.

Family **ASAPHIDAE** Burmeister, 1843

Subfamily **ASAPHINAE** Burmeister, 1843

Genus ***PTYCHOPYGE*** Angelin, 1854

TYPE SPECIES. *Asaphus angustifrons* Dalman, 1827.

Ptychopyge elegans sp. nov.

(Pl. 12, figs. 1, 2, 3 ?, 10–12)

DIAGNOSIS. Outline of combined glabella and occipital ring rounded anteriorly, constricted medially, almost opposite large, semicircular palpebral lobes. Low median ridge extends from large tubercle or boss sited just in front of faint occipital furrow. Frontal area large, slightly concave, with median length about one-quarter that of cranidium. Anterior branches of facial suture weakly sigmoidal and meet frontally at slightly obtuse angle.

HOLOTYPE. BM. It.7973 (Pl. 12, figs. 1, 10–12).

PARATYPE. BM. It.7974 (Pl. 12, fig. 2).

DESCRIPTION. The species is known with certainty from only two isolated cranidia. The median length of the larger is more than four-fifths of the basal breadth. The glabella is of low convexity both longitudinally and transversely, and its outline is rounded frontally but slightly constricted at a point one-quarter the length from the occipital furrow. The sides of the glabella are bounded by axial furrows that are broad and moderately deep both posteriorly and anteriorly but become shallower opposite the palpebral lobes and are continuous with the preglabellar furrow, which becomes semiobsolete medially. The short (*sag.*) occipital ring is poorly defined, separated from the glabella by a broad (*sag.*), shallow occipital furrow immediately in front of which, on the larger specimen, the hindmost portion of the glabella is swollen to form a large, bluntly pointed boss, its apex linked to the front of the glabella by a low, longitudinal, median ridge. On the smaller cranidium (Pl. 12, fig. 2) the corresponding swollen portion of the glabella is less tubercle-like and forms a transverse ridge at the sagittal line. The same specimen lacks the median ridge on the glabella, though there is a suggestion of a small median swelling on the preglabellar field. Glabellar lobes are indistinctly developed but the larger cranidium carries faint traces of 1p and 2p lobes, especially the latter, which are sited opposite the centre of the eyes. The palpebral lobes are conspicuous, semicircular in plan with flattened dorsal surfaces gently declined adaxially, and each carries a shallow palpebral furrow. They are sited a short distance behind centre of the glabella, the breadth of which equals slightly less than half the distance across the palpebral lobes. The anterior branches of the facial suture diverge gently forwards from the eyes, at first slightly more divergent than the axial furrows, but then curve adaxially so that they are subparallel opposite the front of the glabella, and finally arch inwards more strongly and flex forwards to meet frontally at slightly more than a right-angle. The median length of the frontal area equals one-quarter that of the cranidium. There is no distinct division into preglabellar field and anterior border, though the latter is suggested by a slight thickening of the frontal half of the frontal area. As noted earlier, the preglabellar furrow of the holotype is somewhat effaced medially, so that glabella and preglabellar field appear to coalesce, and this feature is still more strongly developed in the small cranidium, where a median elevation traverses the anterior area longitudinally.

A single, small, associated hypostoma from locality B.651 (BM. It.7975, Pl. 12, fig. 3) lacks the posterior wings but is otherwise appropriate for the genus and is referred questionably to *Ptychopyge elegans*. The almost oval median body has a maximum breadth slightly more than two-thirds the length and is divided into unequal lobes by a median furrow that is well defined only laterally. The remaining right anterior wing is broad, extends about half the length of the median body and ends in a well-rounded tip. The specimen generally resembles several hypostomata figured by Balashova (1964 : pl. 1) but no detailed comparison is possible.

DIMENSIONS (in mm).

	BM. It.7973	BM. It.7974
Basal breadth of cranidium	12·6 estd	–
Median length of cranidium	11·3 estd	–
Median length of frontal area	2·9	–
Max. breadth of glabella	3·9	2·5
Distance across palpebral lobes	8·8	5·0 estd

DISCUSSION. In a recent paper Balashova (1964) subdivided *Ptychopyge* sensu lato and erected three additional genera, *Metaptychopyge*, *Paraptychopyge* and *Pseudoptychopyge*. The present material from the Sobova Formation is insufficient for detailed assessment, but its generic position is at least close to, if not identical with, *Ptychopyge* sensu stricto. The glabella of *Ptychopyge rossica* Balashova (1964 : 27, see especially pl. 7, fig. 1 ; pl. 8, fig. 5) has a median ridge apparently ending at the median tubercle, but there are more indications of glabellar lobation, the front of the glabella is better defined, the frontal area is shorter, and the anterior branches of the facial suture are more strongly sigmoidal. *Ptychopyge broeggeri* Schmidt (1904 : 42, pl. 6, figs. 5–8 ; see also Balashova 1964 : 26, especially pl. 5, figs. 2–6; pl. 6, figs. 4, 6, 7) has an equally long frontal area, but differs in that the frontal glabellar lobe is more expanded in outline, a median ridge is absent and the eyes are set closer together. None of the species described by Balashova has the median tubercle so strongly developed as has the Turkish species. Similar features distinguish *P. elegans* from the type species, *Ptychopyge angustifrons* (Dalman) of Lower Ordovician age in the East Baltic region (see Schmidt 1904 : 34, pl. 5, figs. 4, 5, 7–10 ; also Jaanusson *in* Moore 1959 : Fig. 250, 2a–d).

Subfamily **NIOBINAE** Jaanusson, 1959

Genus ***NIOBE*** Angelin, 1851

TYPE SPECIES. *Asaphus frontalis* Dalman, 1827.

Niobe sobovana sp. nov.

(Pl. 10, figs. 1, 3, 10, 11 ; Pl. 11, figs. 1, 3, 5, 6, 9)

DIAGNOSIS. *Niobe* with sides of glabella slightly constricted in front of pair elongated, semielliptical alae. Frontal glabellar lobe broadly rounded anteriorly ; sides straight anterolaterally, converging gently forwards. Traces of four pairs glabellar furrows on internal mould. Palpebral lobes sited opposite 3p and anterior half 2p lobes. Anterior border apparently flat, but poorly defined triangular areas situated laterally on cranidium suggest presence of incomplete preglabellar field. Hypostomal outline widens posteriorly ; posterior margin deeply indented. Middle body straight-sided, divided into two unequal lobes. Pygidium poorly known, but at least four pairs pleural ribs present ; pleural furrows die out on broad pygidial border.

HOLOTYPE. BM. It.7961 (Pl. 10, figs. 1, 3, 10, 11).

PARATYPES. BM. It.7964 (Pl. 11, fig. 1), It.7966 (Pl. 11, figs, 3, 6), It.7968 (Pl. 11, fig. 5), It.7971 (Pl. 11, fig. 9).

LOCALITY AND HORIZON. The species has been found only at locality B.651 at the Sobova Valley section, in the limestone member of the Sobova Formation.

DESCRIPTION. The glabella is large and of low convexity, with maximum breadth equal to five-sixths of the median length. The line of maximum breadth is set slightly in front of centre of the glabella, and farther forwards the frontal glabellar lobe narrows to a broadly rounded anterior margin. The sides of the frontal glabellar lobe have a strikingly truncated appearance and are notably straight, converging gently forwards. Behind the line of maximum breadth the glabellar outline narrows slightly until halfway to the occipital furrow, when it broadens again slightly, though the basal breadth is slightly less than the maximum. The occipital ring is of even length (*sag.*), about one-tenth that of the glabella, from which it is separated by a transversely straight occipital furrow that is deep over its median half but markedly shallower near the axial furrows. The latter are narrow and shallow for the most part, becoming still shallower posteriorly, where an elongated, sub-semi-elliptical ala is sited on the innermost portion of each fixigena. The length of the alae is one-quarter that of the glabella and they extend backwards slightly behind the line of the occipital furrow. The small fragment of exoskeleton remaining on the glabella shows no trace of glabellar furrows, but the internal mould has four pairs of corresponding shallow impressions, separated by a median band about one-third the breadth of the glabella. The 1p glabellar furrows are not easily visible, being little more than a pair of shallow indentations on the glabellar surface opposite the front of the alae. The 2p furrows are almost transverse in direction, gently arched forwards, and do not reach the axial furrows ; they are placed about five-eighths of the distance from front to back of the glabella. The 2p glabellar lobes are the largest of the four pairs and slightly bigger than those of the 1p pair. The 3p furrows curve gently backwards abaxially, converging sharply with the 2p furrows although, like the latter, they do not attain the axial furrows. The 3p lobes are thus subtriangular in outline and occupy adaxially about one-fifth of the length of the glabella. The 4p lobes are the smallest, about half the size of the 3p lobes and delimited frontally by short (*tr.*), straight 4p glabellar furrows that are directed abaxially backwards more strongly than the 3p furrows. Each palpebral lobe is slightly more than a semicircle in outline, its flattened dorsal surface gently declined abaxially. The left lobe, preserved as an internal mould, shows a faint palpebral furrow (see Pl. 10, fig. 10) but the surface of the exoskeleton of the right lobe is unfurrowed, though there is a suggestion of its being slightly bevelled towards the margin at that point, coincident with an increase in density of the small perforations that cover the surface of the exoskeleton there. The posterior branches of the facial suture arch backwards posterolaterally and meet the posterior margin of the cranidium at right-angles. The posterior half of each fixigena is broader (*tr.*) than long and carries a deep, straight posterior border furrow which is transversely in-line with the occipital furrow and delimits a narrow (*exsag.*) posterior border that becomes slightly broader abaxially. Only the hindmost portions of the anterior branches of the facial suture are preserved, and these diverge widely from the eyes, as in other members of the genus. The frontal glabellar lobe is separated by a shallow preglabellar furrow from the incomplete preglabellar field and anterior border. The two latter appear to be fused together for the most part but their lateral extremities show some differentiation, with the preglabellar field forming a pair of slightly convex triangular areas that carry a few large, low tubercles and die out adaxially (see Pl. 10, fig. 1). As noted earlier, only a little of the cranidial exoskeleton remains, but even this exhibits some variety of ornamentation. The surface of the median portion of the frontal glabellar lobe is covered with small perforations, closely grouped but with no obvious arrangement. Anterolaterally there are in addition numerous low, discontinuous ridges which form broken, curved lines subparallel to the sides of the glabella. In cross-section the ridges are asymmetrical, each steeper side facing adaxially and having a line of perforations arranged along its base. The disposition of these structures is shown in Pl. 10, fig. 1 and although their purpose is not clear, the rows of perforations may well have housed small sensory hairs. The anterior border is pitted like the centre of the frontal glabellar lobe but, as described above, the small anterolateral areas assigned to the preglabellar field carry a few large tubercles as well as perforations.

A single, large, left librigena (Pl. 11, fig. 1) is characteristic for the genus, with a blunt, slightly obtuse genal angle sited well outside the posterior branch of the facial suture. Below the incomplete eye surface is a narrow eye platform, bounded by a narrow incised furrow from which the dorsal surface declines to a slightly concave border, defined anteriorly by a lateral border furrow that dies out posterolaterally. The distal portions of the surface, both laterally and posterolaterally, are ornamented by subparallel anastomosing ridges that intersect the anterolateral margin at an acute angle ; behind the genal angle the corresponding ridges meet the posterior margin at right-angles.

Three incomplete hypostomata show the form characteristic of *Niobe*. The most complete has a median length slightly less than the maximum breadth, measured across the posterior wings, from which the breadth decreases anteriorly. The surface of the exoskeleton is ornamented with anastomosing ridges which generally run transversely. The large middle body occupies more than half the overall breadth and, especially on the internal mould, is seen to be divided into two unequal lobes. Of these the anterior lobe is much the larger, broadly rounded frontally, straight-sided, and bluntly pointed posteriorly where it is terminated by a median furrow that is shallow centrally but deepens laterally to form a pair of conspicuous notches. The internal mould of the posterior lobe (see especially Pl. 11, fig. 5) is transversely straight medially but forms a pair of slightly swollen projections that are directed posterolaterally and separated by a deep notch in which the ornamenting ridges run parallel to the indentation of the bifurcated hypostomal margin. The posterior wings, separated by a pointed median notch, are large and flattened, well rounded in outline and diminish frontally to a narrow rim which then expands to form the anterior wings.

The thorax is not known with certainty but a fragmentary pleura of asaphid type (Pl. 11, fig. 10) has a deep, narrow pleural furrow that dies out approximately halfway to the tip, and bears some resemblance to the structure of the pygidium assigned to *Niobe sobovana*. The doublure is ornamented with strong terrace-lines and the tip forms a broad, falcate spine, directed backwards. The specimen is too fragmentary for certain identification and is figured as Asaphid gen. et sp. undetermined.

An associated incomplete large pygidium (Pl. 11, fig. 9) is assigned to this species. It is sub-semicircular in outline, with maximum breadth estimated at about twice the median length, and well rounded anterolaterally. The axis although fragmentary was evidently relatively slender with almost straight sides that converged gently backwards. The surviving left pleural region has an anterior half-rib followed by four well-defined ribs with, probably, room for one more. The pleural field has a prominent boundary and stands higher than the well-defined, broad pygidial border. Narrow pleural furrows are deeply incised on the pleural field but become shallow and narrower across the pygidial border and die out a short distance from the margin. The internal mould shows low tubercles covering the pleural ribs. Part of the external mould of the pygidial doublure is exposed ; it is as broad as the border of the dorsal exoskeleton and ornamented with about eleven or twelve conspicuous, subparallel terrace-lines.

Another incomplete pygidium, BM. It.7967 (Pl. 11, fig. 4), from the same horizon and locality, differs from Pl. 11, fig. 9 in being proportionately longer, whilst the border is relatively narrower and is not traversed by the pleural furrows. In addition to the anterior half-ribs there are five well-defined pairs of ribs and traces of a sixth pair. The straight-sided narrow axis carries traces of at least eight axial rings and extends backwards only as far as the inner margin of the pygidial border. This specimen is referred questionably to *Niobe.*

DIMENSIONS (in mm, IM = internal mould, EM = external mould).

	It.7961	It.7966	It.7968	It.7971
Length of glabella	20·6 estd (IM)	–	–	–
Max. breadth of glabella	17·3 (EM)	–	–	–
Min. breadth of glabella	12·8 estd (IM)	–	–	–
Basal breadth of glabella	14·8 (IM)	–	–	–
Distance across palpebral lobes	21·8 (EM)	–	–	–
Overall length of hypostoma	–	9·4 (IM)	–	–
Overall breadth of hypostoma	–	8·4 estd (IM)	11·2 estd (IM)	–
Length of median body	–	8·0 estd	–	–
Max. breadth of median body	–	5·6 (IM)	7·0 estd (IM)	–
Breadth of pygidium	–	–	–	20·0 estd (IM)
Length of pygidium	–	–	–	11·5 estd

DISCUSSION. The merits of the various features whereby *Niobe* may be distinguished from the closely related genus (or subgenus) *Niobella* Reed (1931 : 462) have been discussed by Whittington (1965 : 348). To summarize, the hypostoma of *Niobe frontalis* has a deep median notch in the posterior margin, whereas that of *Niobella homfrayi*, type species of the genus, has the outline tapered backwards and the posterior margin is rounded. The difference was regarded as important by Lake (1942 : 328–30), though he preferred to retain *Niobella* only as a subgenus of *Niobe*. Later Tjernvik (1956 : 223–4) separated the two as genera on the basis of the pygidium, that of *Niobe* having pleural ribs that expand abaxially and terminate in-line with the inner margin of the border and beyond that of the broad doublure whilst that of *Niobella* has the pleural regions smooth or slightly furrowed, the ribs ending at the narrow doublure. Although Jaanusson (*in* Moore 1959 : O 350) followed the same course, Whittington (1965 : 349) found the arrangement unsatisfactory as it entails an artificial grouping together of forms with distinct types of hypostoma. Whittington justified the inclusion of *Niobe quadraticaudata* (Billings 1865), from the Table Head Formation of western Newfoundland, in that genus mainly on the basis of the hypostoma, but drew attention also to the role of the alar lobes as being of possible significance. The new Turkish species clearly belongs to *Niobe* on the basis of the glabellar outline, hypostoma and alae, and these are taken as being more significant than the associated pygidium which, with its pleural ribs that are not strongly convex at their distal ends but are separated by pleural furrows that partially cross the wide border, does not exactly match the pygidium of the type species.

Asaphid genus and species undetermined

(Pl. 11, figs. 2, 8, 10 ; Pl. 12, figs. 5–9)

Under this heading are grouped several asaphid fragments which are too immature or too fragmentary to be named satisfactorily.

BM. It.7978 (Pl. 12, figs. 7, 9) from the Sobova Formation at locality C.429 represents an originally large pygidium of depressed form with a narrow, almost straight-sided axis, well segmented by transversely straight ring furrows. The pleural regions comprise at least five and a half pairs of ribs (there is room for six or seven pairs), separated by well-defined, straight pleural furrows which are only slightly deeper than the interpleural furrows. The latter divide the ribs into subequal anterior and posterior bands, and die out approximately half-way to the margin ; the pleural furrows extend a little farther but leave a notably wide, smooth border. The doublure, though not completely visible, is conspicuously wide, ornamented by numerous closely spaced terrace-lines, those near the inner margin appearing gently waved in plan. Detailed comparison is not practicable, but the general configuration compares with that of *Opsimasaphus* (*Nobiliasaphus*) *nobilis repulsus* Přibyl & Vaněk (1968 : 192, pl. 1, fig. 7) from the Dobrotivá Formation, Llandeilo Series, of Bohemia. The latter has a very wide doublure and the pleural ribs are of similar shape and size, as are the axial rings, as far as can be judged, but differs in that the anterior and posterior bands of the ribs are of more unequal breadth (*exsag.*).

BM. It.7970 (Pl. 11, fig. 8) from the same locality is a small hypostoma approximately 3 mm broad (excluding anterior wings) preserved as an internal mould. The incomplete posterior wings are separated by a broad median notch in which the posterior margin forms a gentle convex curve. The median body extends the whole of the median length of the hypostoma and is of low convexity, divided by a shallow, median furrow into two markedly unequal lobes, the posterior of which is crescentic in plan and ends anterolaterally in a pair of sharply defined maculae.

The remaining figured specimens are all from the limestone member of the Sobova Formation at locality B.651. An incomplete hypostoma, BM. It.7965 (Pl. 11, fig. 2), lacks the posterior margin and the hindmost parts of the posterior wings. The outline of the median body, the lateral development of the median furrow and the narrow anterior portions of the posterior wings are generally similar to those of *Ptychopyge* and related genera, but the specimen differs in that the posterior lobe of the median body is convex and its rear margin well defined. BM. It.7977 (Pl. 12, fig. 5) forms part of a large thoracic segment, the left pleura of which is divided by a deep, narrow (*exsag.*) pleural furrow into unequal bands, the anterior one of ridge-like form and much the narrower. The dorsal surface is ornamented with densely crowded ridges that run subparallel to the axis of the thorax and traverse the pleural furrow.

Two very small pygidia are clearly immature although one of them, BM. It.10660 (Pl. 12, fig. 6) with length 1·4 mm and breadth 3·2 mm, has a relatively small number of pleural ribs and axial rings, four and a half and four respectively, and may represent an early holaspid stage. The posterior margin of this specimen is gently rounded in outline, the doublure is moderately wide, whilst the flat pleural regions are traversed by pleural and interpleural furrows which curve strongly back towards, and almost reach, the lateral margins. The generic position is not determinable but the small number of pleural ribs is suggestive of that on the large pygidium figured elsewhere in this paper as *Niobe sobovana* (Pl. 11, fig. 9), and the specimen is clearly very different from another small pygidium of approximately similar breadth (Pl. 12, fig. 8). The latter, BM. It.7980, is proportionately longer, the large axis has traces of at least ten axial rings, and the pleural regions are composed of five well-differentiated pleurae followed by almost unfurrowed areas behind the line of the fifth ring furrow. If truly an asaphid, the pygidium may represent a Meraspis Degree 2, but its systematic position is uncertain.

Family Unknown

Genus and species undetermined A

(Pl. 7, figs. 2, 4, 9)

FIGURED SPECIMEN. BM. It.7944.

LOCALITY AND HORIZON. B.651 at the Sobova Valley section, in the limestone member of the Sobova Formation.

DESCRIPTION. An incomplete pygidium with length and estimated breadth of 2·2 mm and 6·0 mm respectively is transversely semielliptical in outline. Frontally the strongly convex axis occupies one-third of the overall breadth and its straight sides converge gently to a blunt terminal piece which extends almost as far as the posterior margin and is linked to the latter by a low post-axial ridge. There is a slightly thickened border which narrows (*sag.*) posteriorly and is gently arched below the post-axial ridge (see Pl. 7, fig. 4). The axis has two well-defined, transversely straight axial rings which are almost equisized and together occupy half the axial length, followed by a smaller, weakly defined third ring. The pleural fields carry a pair of anterior half-ribs which are transversely straight for half their length and then curve strongly backwards posterolaterally. These are followed in turn by a pair of strongly developed ribs impressed by faint interpleural furrows, a pair of subtriangular raised areas representing the second ribs, and a pair of low, subcircular protruberances indicating the third ribs. All the ribs are separated by broad (*exsag.*) pleural furrows, and the surface of at least the first pair of ribs is ornamented with small, closely spaced granules.

DISCUSSION. Although unassigned, the pygidium bears some resemblance to that of *Euloma* which also is almost straight frontally, with an axis of comparable size and three pairs of pleural ribs that show a corresponding diminution. However, the pygidium of the type species, *E. laeve* Angelin (see Tjernvik 1956 : 274), has conspicuously large articulating facets, the ribs are narrower (*exsag.*) and much straighter, and no post-axial ridge is visible.

Genus and species undetermined B

(Pl. 9, fig. 6)

FIGURED SPECIMEN. BM. It.7960.

LOCALITY AND HORIZON. C.429, 1·5 km east of Kızılca, in crystalline limestones of the Sobova Formation.

DESCRIPTION. A single small pygidium preserved as an internal mould is subsemielliptical in outline with median length 3·6 mm and maximum breadth 5·7 mm. The axis, with frontal breadth 1·8 mm, is relatively narrow, has straight sides and tapers gently to the apparently subrounded tip. There are three well-defined, transversely straight axial rings with a fourth ring less clearly developed; the remainder of the axis is not preserved. The proximal portions of the pleural regions are higher and more convex than the wide, smooth border, and carry two pairs of short (*tr.*), unfurrowed ribs in addition to an incompletely preserved pair of anterior half-ribs. The systematic position of the specimen is not clear, but it does not belong with any of the other genera found at locality C.429.

III. AGE AND AFFINITIES OF THE TRILOBITES

Earlier provisional faunal lists for the Sobova Formation (Dean & Monod 1970 : 423, 424) contained relatively few trilobite genera, but the present work has enabled the number to be augmented as follows:

Locality B.651. *Agerina*, *Ampyx*, *Apatokephalus*, *Carolinites*, cheirurid gen. undet., *Geragnostus*, *Harpides*, *Illaenus*, *Metopolichas*, *Niobe*, *Panderia*, *Phillipsinella*, *Protostygina*, *Pseudopetigurus*, *Pterygometopus* ?, *Ptychopyge*, *Sobovaspis*, *Symphysurus* and *Trinodus*.

Locality B.652. *Symphysurus* only.

Locality C.429. *Euloma* (*Lateuloma*), *Geragnostus*, harpidid gen. indet., *Nileus*, *Pliomerina*, *Pricyclopyge* and *Symphysurus*.

Locality C.432. *Euloma* (*Lateuloma*), *Geragnostus* and *Symphysurus*.

On the basis of their affinities with the various Ordovician faunal provinces, these genera may be divided into a number of groups although, as will be seen, some do not fall readily into such categories but are not sufficiently widespread to be termed cosmopolitan.

(a) *Genera of predominantly Tethyan type*

As discussed elsewhere (Dean 1967), Tethyan trilobite faunas comprise those of the Mediterranean region, the Anglo-Welsh area, France, Spain, Portugal, northwest Africa, much of southern and southeastern Europe and parts of the eastern coastal region of North America. They include so-called 'Bohemian faunas' as well as Whittington's (1966a) '*Selenopeltis* fauna'. Their horizontal distribution varied considerably at different times within the Ordovician period, but in early Arenig times, at least, they extended eastwards relatively unchanged in composition to southeastern Turkey and occurred, with some modification, still farther east in southern China.

Genera of this type are conspicuous in the underlying Seydişehir Formation but then undergo a sudden, marked reduction and are poorly represented in the Sobova Formation, coincident with a marked lithological change from mudstones and shales to fragmental limestones. *Pricyclopyge* is well documented in Anglo-Welsh and Bohemian faunas which range in age from Arenig to Llandeilo Series, but was not entirely confined to the Tethyan region, as is shown by its record from the Upper Tremadoc of Sweden. It is particularly unfortunate that trinucleid trilobites are so rare in the Sobova Formation, being represented by only a few fragments at B.651. Members of the family have proved of great value in Ordovician correlation but the Sobova material cannot be assigned even generically. The presence of two E arcs of pits on the cephalic fringe is of some interest but little significance as similar structures are known nowadays from Ordovician rocks as early as Lower Arenig in age in the Anglo-Welsh area, whereas it was at one time believed that a marginal girder indicated the most primitive stage of development, followed by the addition of further development of additional E arcs in successively higher strata. The affinities of the incomplete pliomerid, if correctly assigned to *Pliomerina*, lie with an eastern Tethyan element. The resemblance of one pygidium to that of the Bohemian Llanvirn genus *Protostygina* has been noted; more secure evidence of Bohemian affinities is afforded by the single cranidium of *Pseudopetigurus*, a rare genus even in its type area, where it is restricted to the Upper Arenig, but a member of a family, the Bathyuridae, which was widely distributed beyond the bounds of Tethyan faunas.

(b) *Genera of predominantly Balto-Scandinavian type*

Nileus, *Niobe* and *Ptychopyge* are all common in Balto-Scandinavian faunas but the first two have a westerly extension into eastern North America where they may be found as high as the Lower Llanvirn Series. The bathyurid *Agerina* was previously best known from Scandinavia, the East Baltic region and Bornholm, whilst the illaenid *Panderia* is an essentially Balto-Scandinavian form, though recorded in Asia from the Karakorum Range in company with a Baltic-type fauna. The small trilobite referred here to *Phillipsinella* is a member of a genus which was widely distributed in Ashgill times, but all records from pre-Ashgill rocks are in faunas of Balto-Scandinavian type, so its presence at Sobova is not altogether surprising. Tripp's (1958 : 575) records of *Metopolichas* show the genus to be almost exclusively of Balto-Scandinavian type and of Lower and Middle Ordovician age. In Scandinavia its lowest occurrence is in the Expansus Limestone and the stratigraphical implications of its appearance there are noted later. *Euloma*, although based on a Scandinavian type species, is widespread in early Ordovician strata, having been found in Europe, the Anglo-Welsh and Mediterranean areas, and as far afield as central North America, though it is doubtful whether it may be termed truly cosmopolitan. The new subgenus *E.* (*Lateuloma*) has not yet been found with certainty outside Turkey.

(c) *Genera of cosmopolitan distribution*

Perhaps the most obvious of these is *Geragnostus* ; its type species was described originally from the Tremadoc Series of Sweden but the genus may range as high as the Ashgill Series and its distribution is almost world-wide. Similarly *Trinodus*, first found in the Arenig of Sweden and southern France, subsequently has a long history and attained a particularly wide distribution in Ashgill times. *Harpides* is known first from the Tremadoc Series and most of its representatives appear to be of early Ordovician age, though the latest species is probably *H. atlanticus* (Billings) from the Lower Llanvirn Series of western Newfoundland. In Sweden the genus is known from both Tremadoc and Lower Arenig Series, whilst Dr Valdar Jaanusson informs me (personal communication) that *H. plautini* Schmidt is from the Upper Arenig, Volkhovian Stage in part, of the Leningrad District. *Apatokephalus* is perhaps best known from Scandinavia, where it provides a zonal species for the highest Tremadoc Series, but it occurs also in both North and South America as well as western Europe. Many of the records are from Tremadoc strata and I am not aware of any post-Arenig occurrences. *Carolinites* is a particularly good example of a cosmopolitan genus, closely similar forms having been recorded from western and eastern North America, East Greenland, western Ireland, western Russia and Kazakhstan as well as Turkey and the type area in Tasmania. None of these occurrences is older than Lower Arenig, and the youngest is Lower Llanvirn Series.

Although nearly all the recognizable trilobite species from the Sobova Formation are new, the above discussion of the genera present demonstrates that their most marked affinities are with faunas of the Balto-Scandinavian region. The latter are best known from the works of Bohlin, Tjernvik, Jaanusson and V. Poulsen, whose stratigraphical subdivisions and faunas are now discussed. The trilobites of locality C.429 are considered separately, as the stratigraphical relationships there are less clear.

The age of the trilobites at locality B.651

In his description of the so-called Asaphus Limestone and adjacent strata of northernmost Öland, Bohlin (1949) established the following ascending succession of trilobite zones: *Megalaspis planilimbata, Megalaspis limbata, Asaphus lepidurus, Asaphus expansus, Asaphus raniceps, Megalaspis centaurus, Megalaspis gigas* and *Asaphus platyurus.* Of these, the zones of *Asaphus lepidurus, A. expansus* and *A. raniceps* make up the Asaphus Limestone. The genus *Megalaspis* has since been renamed *Megistaspis.* Trilobite familes and genera listed from the Asaphus Limestone by Bohlin (1949 : 566, 567) and later revised by him (1955) and other authors are as follows: Pterygometopidae (*Pterygometopus*), Cheiruridae (*Ceraurinella, Cyrtometopus, Acanthoparypha, Sphaerocoryphe*), Pliomeridae (*Pliomera*), Encrinuridae (*Cybele*), Odontopleuridae (*Boedaspis*), Lichidae (*Lichas, Conolichas,* both these genera represented by species that are now assigned to *Metopolichas*), Harpidae (*Harpes*), Remopleurididae (*Remopleurides*), Asaphidae (*Asaphus, Homalopyge, Megistaspis, Niobe, Pseudasaphus, Ptychopyge*), Nileidae (*Nileus, Symphysurus*), Illaenidae (*Illaenus*), Raphiophoridae (*Ampyx*) and Agnostidae (*Trinodus*).

The faunal lists given by Bohlin for the zone of *Asaphus raniceps* and the zone of *A. expansus* are used as the basis of comparison in Table I and give values of 35 and 55 respectively for the Index of Faunal Resemblance at B.651. Notable absentees from these Swedish strata are *Agerina, Apatokephalus* and *Harpides,* but the first appearance of *Metopolichas* and *Illaenus* must be considered an even more important feature of the fauna. The age of the Asaphus Limestone has been placed approximately in the range Upper Arenig (in part) and lowest Llanvirn Series by Jaanusson (1960 : 346) and its relevance to that of the Sobova Formation is noted later.

Stratigraphy and trilobite faunas of particular relevance to those of the Sobova district were described from Sweden by Tjernvik (1956 : 112, 277) whose comprehensive work on the Planilimbata Limestone (Arenig Series) and its subdivisions provided the following data. Some of the generic names used originally by Tjernvik have been modified in the light of later researches.

Subdivision B.4. Zone of *Megistaspis estonica*

Agerina, Ampyx, Asaphus, Cyrtometopus, Euloma, Geragnostus, Harpides, Lonchodomas, Megalaspides, Megistaspis, Menoparia ?, Nileus, Niobella, Raymondaspis, Remopleuridiella, Selenoharpes, Sphaerexochus ?, Symphysurus.

Subdivision B.3. Zone of *Megalaspides dalecarlicus*

Ampyx, Diaphanometopus, Dysplanus ?, Euloma, Geragnostus ?, Harpides, Megalaspides, Nileus, Niobella, Plesiomegalaspis, 'Protopliomerops', Raymondaspis, Selenoharpes.

Subdivision B.2. Zone of *Megistaspis planilimbata*

Ampyx, Apatokephalus, Borogothus, Cyclopyge, Diaphanometopus, Dysplanus ?, Ekeraspis, Euloma, Geragnostus, Harpides, Ischyrophyma, Lannacus, Lapidaria,

Table I

Comparison of the trilobite fauna from the limestone member of the Sobova Formation at locality B.651 with others of approximately similar age in Scandinavia using Simpson's Index of Faunal Resemblance.

Genera present in limestone member of Sobova Formation at locality B.651 (doubtful genera are omitted from calculations)		Asaphus Lst., northernmost Öland, Faunal List I of Bohlin (1949), incl. *Asaphus raniceps*	As above. Faunal List II of Bohlin (1949), incl. *A. expansus*	Skelbro Limestone, Bornholm. From V. Poulsen (1965)	Sweden, after Tjernvik (1956)				
					B.4. Zone of *Megistaspis estonica*	B.3. Zone of *Megalaspides dalecarlicus*	B.2. Zone of *Megistaspis planilimbata*	B.1. Zone of *Megistaspis armata*	A.6. Zone of *Apatokephalus serratus*
Agerina		–	–	?	×	–	–	–	×
Ampyx		×	×	×	×	×	×	×	–
Apatokephalus		–	–	–	–	–	×	×	×
Carolinites		–	–	–	–	–	–	–	–
Geragnostus		–	–	×	×	×	×	×	×
Harpides		–	–	×	×	×	×	×	×
Illaenus		×	×	–	–	–	–	?	–
Metopolichas		×	×	?	–	–	–	–	–
Niobe		×	×	–	–	–	×	×	×
Panderia		–	–	×	–	–	×	–	×
Phillipsinella . . .		–	–	–	–	–	–	–	–
Protostygina . . .		–	–	–	–	–	–	–	–
Pseudopetigurus . . .		–	–	–	–	–	–	–	–
Pterygometopus ? . .		×	×	–	–	–	–	–	–
Ptychopyge		×	×	?	–	–	–	–	–
Sobovaspis		–	–	–	–	–	–	–	–
Symphysurus		–	×	×	×	–	×	×	×
Trinodus		×	–	–	–	–	×	–	×
Total genera in deposit .	17	20	11	17	16	10	27	19	23
Index of Faunal Resemblance	–	35	55	24	31	33	41	35	41

Leiagnostus, Megistaspis, Nileus, Niobe, Niobella, Orometopus, Ottenbyaspis, Pliomerops, Raymondaspis, Remopleurides, Selenoharpes, Shumardia, Symphysurus, Trinodus, Varvia.

Subdivision B.1. Zone of *Megistaspis armata*

Ampyx, Apatokephalus, Borogothus, Euloma, Falanaspis, Geragnostus, Harpides, Hunnebergia, Illaenus ?, Lapidaria, Megistaspis, Nileus, Niobe, Orometopus, Platypeltoides, Pliomerops, Saltaspis, Shumardia, Symphysurus, Varvia.

Subdivision A.6. Zone of *Apatokephalus serratus* (Tremadoc Series)

Agerina, Apatokephalus, Borogothus, Ceratopyge, Dikelokephalina, Euloma, Geragnostus, Harpides, Nileus, Niobe, Niobella, Niobina, Orometopus, Ottenbyaspis, Parabolinella, Parapilekia, Peltura ?, Pricyclopyge, ' Protopliomerops ', Saltaspis, Shumardia, Symphysurus, Triarthrus, Trinodus, Varvia.

It will be seen at once that certain Sobova genera absent from the ' Asaphus Limestone ' are present in Tjernvik's lists, but application of the Index of Faunal Resemblance produces some varied results for locality B.651 (see Table I). The highest value of 41 occurs not only at the horizon of A.6, the highest zone of the Tremadoc Series, but also again in Zone B.2, with diminutions at B.1 and again from B.3–4, though such fluctuations could well be explained by variations in local ecological conditions. Genera such as *Agerina, Apatokephalus, Harpides* and *Ottenbyaspis* (which closely resembles *Panderia monodi* sp. nov.) may occur in the Swedish Upper Tremadoc, but such an age for the rocks at locality B.651 cannot be contemplated for various reasons : (a) the Sobova Formation overlies with apparent conformity the Seydişehir Formation, in the upper part of which *Didymograptus* and *Tetragraptus* suggest the presence of the Extensus Zone ; (b) several genera at B.651 are not known from pre-Arenig strata ; and in particular *Metopolichas* and *Pseudopetigurus* are not recorded from below the Upper Arenig. Similarly although Tjernvik's B.2, the zone of *Megistaspis planilimbata*, is a more reasonable proposition in that it provides his highest recorded *Apatokephalus* and *Ottenbyaspis*, nevertheless it represents an horizon that is too low for *Metopolichas* and *Illaenus*.

The presence of *Metopolichas* suggests that, also by analogy with the Balto-Scandinavian region, the fauna at B.651 cannot be older than the upper half of the Arenig Series. Application of the Index of Faunal Resemblance to the Asaphus Limestone of Sweden (see Table I) produces values no higher than those for the Lower Arenig noted above, and it may be that the method has limitations when applied to such widely separated trilobite faunas. On the other hand, the lowest of the Swedish strata assigned to the Asaphus Limestone mark the lowest range of both *Metopolichas* and *Illaenus* according to the lists of Warburg (1939) and Bohlin (1949), an observation kindly confirmed by Dr Valdar Jaanusson (personal communication), and the occurrence of these genera at B.651 may be regarded as stratigraphically significant. Some of the Sobova genera range upwards into Llanvirn strata in other parts of the world, but a genus such as *Apatokephalus* has not been recorded from post-Arenig rocks, whilst *Pseudopetigurus* is closest to a species in the Upper Arenig.

On balance, therefore, the trilobites at locality B.651 are unlikely to be Lower Arenig or post-Arenig in age, but the evidence for an horizon within the Upper Arenig is imprecise. Conodonts from this locality and horizon are now being studied by Dr C. R. Barnes whose preliminary determinations (personal communication) show that the fauna is of Swedish type and Volkhovian age. In current stratigraphical terminology the Volkhovian includes at the base the highest trilobite zone of those making up the Extensus Zone or Lower Arenig, and at the top the lowest of the three trilobite zones forming the Asaphus Limestone, i.e. the *Asaphus lepidurus*

BRITISH SERIES OF THE ORDOVICIAN	BRITISH GRAPTOLITE ZONE	NORWEGIAN GRAPTOLITE ZONE	SWEDISH GRAPTOLITE ZONE	STRATIGRAPHICAL SUCCESSION IN SOUTHERN SWEDEN AND THE BALTIC REGION, BASED ON THE WORKS OF JAANUSSON, POULSEN & TJERNVIK					SUCCESSION IN BEYŞEHİR REGION	
				SERIES	STAGE	SUBSTAGE	LITHOLOGICAL SUBDIVISIONS PREVIOUSLY EMPLOYED	ZONAL TRILOBITE	SOBOVA VALLEY	KIZILCA ,AREA
LLANVIRN (PARS)	Didymograptus bifidus	Didymograptus bifidus	Didymograptus bifidus	OELAND	KUNDAN	ALUOJAN	VAGINATUM LST.	Megistaspis gigas	UNCONFORMABLE JURASSIC LIMESTONES	
								Megistaspis obtusicaudata	▨	▨
						VALASTEAN		Asaphus raniceps	▨	▨
ARENIG	Didymograptus hirundo	Isograptus gibberulus	Isograptus gibberulus			HUNDERUMIAN		Asaphus expansus	▨	▨
					VOLKHOVIAN	LANGEVOJAN	LEPIDURUS LST.	Asaphus lepidurus	GREY SHALES FOSS. LSTS OF B. 651 - - - ? - - -	▨ SEYDİŞEHİR FORMATION
						No Name	LIMBATA LST.	?	SEYDİŞEHİR FORMATION	▨
								Megistaspis lata		▨ ?
	Didymograptus extensus							Cyclopyge stigmata		FOSS. LSTS OF C. 429 & C. 432
		Didymograptus extensus	Phyllograptus angustifolius elongatus		LATORPIAN	BILLINGENIAN	PLANILIMBATA LST. Upper	Megistaspis estonica		- - -?- - -
			Phyllograptus densus					Megalaspides dalecarlicus		SEYDİŞEHİR FORMATION
			Didymograptus balticus & T. phyllogr'oides			HUNNEBERGIAN	Lower	Megistaspis planilimbata		
								Megistaspis armata	BASE NOT SEEN ?	BASE NOT SEEN ?
TREMADOC (PARS)							CERATOPYGE LST.	Apatokephalus serratus		

FIG. 5. Table showing the correlation of the Sobova Formation with relevant strata in Sweden and the Baltic region.

Zone. There is thus reasonable agreement between the trilobite and conodont evidence and a tentative correlation of the limestones at B.651 with the *A. lepidurus* Zone would not be unreasonable.

The age of the trilobites at localities C.429 and C.432

Limestones forming part of the Sobova Formation crop out in the vicinity of the village of Kızılca, 17 km north-west of Seydişehir and between 7 and 8 km south-southeast of the section in the Sobova Valley (see Figs. 2, 3). At C.429 six trilobite genera were collected, but specimens, which occur in a white and grey crystalline limestone, are not common. At C.432 the lithology is slightly different, comprising limestones that are grey and a distinctive pink in colour, somewhat cleaved and cut by thin veins of calcite. The fauna here is more sparse even than at C.429 but the occurrence of *Euloma* (*Lateuloma*), *Geragnostus* and *Symphysurus* suggests that the two deposits are of similar age. C.429 and C.432 differ from the limestone member of the type Sobova Formation in both lithology and faunal composition, but it was not immediately obvious whether they represent a younger or an older horizon. It is believed that these Ordovician limestones rest on strata of the Seydişehir Formation near Kızılca but the structural relationships are not clear.

The Index of Faunal Resemblance for the Kızılca trilobites in relation to the Swedish Lower Ordovician genera documented by Tjernvik (1956) is shown in Table II. Some of the values are high, higher in fact than those obtained from the fauna at B.651, and the highest is given by the *Apatokephalus serratus* Zone of the Tremadoc Series, but the reliability of the figures is probably diminished by the small number of genera available at C.429. However, a post-Tremadoc rather than a pre-Arenig age is suggested by the fragment of *Pliomerina*, even though the evidence is scanty. *Euloma*, even in its broad sense, does not occur below the Tremadoc, in which series it is particularly abundant, but does not appear to range higher than the Lower Arenig. On the basis of the trilobites, the limestones of the Sobova Formation at C.429 and C.432 are provisionally assigned to the Lower Arenig, though a more varied fauna is required in order to give a detailed age assessment. Support for this view is provided by the conodonts and Dr C. R. Barnes, who has examined the material from this horizon, submits the following notes (personal communication): 'C.429 yielded only 30 identifiable conodonts. These are predominantly drepanodiform, acodiform and oistoidiform elements previously undescribed. The overall evolutionary development of those elements in C.429, which are certainly of Arenigian age, suggests that this fauna is slightly older than that of B.651.'

The stratigraphy of the Seydişehir Formation in its type area northwest of Seydişehir is not known in detail but at least the upper portion contains Lower Arenig graptolites. Consequently, if the whole of the upper Seydişehir Formation were to be regarded as of Lower Arenig age, the placing of the limestone member of the Sobova Formation at B.651 in the upper half of the Upper Arenig (see Fig. 5) would imply the existence of a disconformity between the two formations. However, the highest beds of the Seydişehir Formation beneath the Sobova Formation in its type area at the Sobova Valley contain inter alia *Symphysurus*, a genus which became

TABLE II

Comparison of the trilobite fauna from limestones mapped as Sobova Formation at locality C.429 near Kızılca (see Figs. 2, 3) with others of approximately similar age in Scandinavia using Simpson's Index of Faunal Resemblance.

Genera present in Sobova Formation at locality C.429		Skelbro Limestone, Bornholm, From V. Poulsen (1965)	Sweden, after Tjernvik (1956)				
			B.4. Zone of *Megistaspis estonica*	B.3. Zone of *Megalaspides dalecarlicus*	B.2. Zone of *Megistaspis planilimbata*	B.1. Zone of *Megistaspis armata*	A.6. Zone of *Apatokephalus serratus*
Euloma		–	×	×	×	×	×
Geragnostus . . .		×	×	–	×	×	×
Nileus		×	×	×	×	×	×
Pliomerina		–	–	–	–	–	–
Pricyclopyge . . .		–	–	–	–	–	×
Symphysurus . . .		×	×	–	×	×	×
Total genera in deposit .	6	17	16	10	27	19	23
Index of Faunal Resemblance	–	50	67	33	67	67	83

still more abundant in the Sobova Formation. To what degree this may be accepted as evidence for a conformable relationship between the two formations at this point is not yet clear, though it receives some support from the occurrence at a nearby locality of possibly Upper Arenig cephalopods (Collins *in* Monod 1967 : 83 ; Dean & Monod 1970 : 422).

Near Kızılca the limestones of the Sobova Formation at localities C.429 and C.432, known to be older than those of B.651, may not be of lowest Arenig age as they overlie strata of the Seydişehir Formation, though the age and lower limit of the latter are not yet confirmed by means of fossils and the presence of a disconformity between the two formations at this point is by no means established. In an earlier account (Dean & Monod 1970 : 423–4) the Arenig limestones of B.651 were thought to be represented at Taraşçı, north-northwest of Seydişehir, by an attenuated limestone sequence, followed by red sandstones which might be the equivalent of the ' grey shales ' of the Sobova Valley. Such conclusions are still provisional as they are not yet substantiated by faunal evidence, and deposition of the Sobova Formation took place under conditions which produced marked lateral changes of facies at a time when faunal links were being established between Scandinavia, the Taurus Mountains and points still farther eastwards along the Tethyan region.

Regnéll (1940 : 13) suggested that a connection between Northern Europe and the Bohemian Basin (better known for its Tethyan or Mediterranean faunal elements of both Cambrian and Ordovician age) existed during part of the Lower Ordovician. The trilobites of the Sobova Formation extend the scope of this hypothesis and suggest that changes in the distribution of areas of marine deposition within the Tethyan region were beginning to take place as early as the Upper Arenig. No evidence of Lower Ordovician marine faunas of Scandinavian type has been found in the Mediterranean region west of Turkey or, to any marked degree, in the Bohemian Basin. However, the easterly extension of such faunas seems well established, and the Sobova trilobites provide an additional link between those of the Balto-Scandinavian region and the Himalayan faunas described by Gortani (1934), which include *Illaenus*, *Nileus* and *Panderia*. In northern Iran the uppermost member of the Mila Formation contains *Illaenus* and orthid brachiopods, and succeeds a member from which Upper Cambrian trilobites, including *Iranaspis*, have been recorded (Stöcklin, Ruttner & Nabavi 1964). It is not clear whether the strata with *Illaenus* are conformable on the Cambrian or whether they represent a higher level within the Ordovician. In eastern Iran the trilobites recorded from the Shirgesht Formation (Winsnes *in* Ruttner, Nabavi & Hajian 1968 : 34, 35) have not yet been described but include *Hystricurus*, *Illaenus*, *Marrolithus* ?, *Megalaspides*, *Ningkianolithus* and *Symphysurus*. Some of these genera have an extended range within the Ordovician but the trinucleids have been documented only from Llandeilo and Caradoc Series, and the fauna should therefore be considerably younger than that of the Sobova Formation.

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W. T. Dean, D.Sc.
Geological Survey of Canada
601 Booth Street
Ottawa KIA OE8
Canada

EXPLANATION OF PLATES

The specimens illustrated are preserved in limestones of the Sobova Formation. Most were coated with a black opaque and then sprayed with a thin film of ammonium chloride prior to being photographed, but in some cases latex casts were prepared from external moulds. For position of fossil localities see Text-fig. 3. The figured material is housed in the British Museum (Natural History) and specimen numbers carry the prefix It. Photographs by the author.

PLATE 1

Geragnostus sp. p. 289

Sobova Formation, locality C.429

FIG. 1. Plan view of fragmentary cranidium. It.7891. × 12.

FIG. 3. Plan view of small pygidium. It.7892. × 12.

Geragnostus semipolitus sp. nov. p. 287

Sobova Formation, locality B.651

FIG. 2. Plan view of incomplete pygidium. Note traces of ornamentation. Paratype. It.7886. × 10.

FIGS. 4, 5, 11. Left lateral, plan and posterior views of pygidium. Holotype. It.7887. × 12.

FIGS. 7, 14, 16. Left lateral, plan and posterior views of cranidium. Paratype. It.7895. × 12.

FIG. 8. Plan view of partly exfoliated cranidium. Paratype. It.7893. × 12.

FIG. 9. Plan view of pygidium. Note diminution of furrows on and around axis, and lack of median tubercle on outer surface. Paratype. It.7888. × 10.

FIG. 10. Incomplete cranidium showing median tubercle and basal glabellar lobes. Paratype. It.7894. × 12·5.

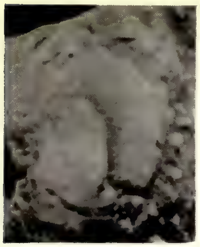
FIG. 12. Partly exfoliated pygidium. Note shape of axis and position of median tubercle. Paratype. It.7889. × 10.

FIG. 17. Plan view of small cranidium. Paratype. It.7896. × 12.

Trinodus hebetatus sp. nov. p. 289

Sobova Formation, locality B.651

FIGS. 6, 13, 15. Left lateral, posterior and plan views of pygidium. It.7890. × 12.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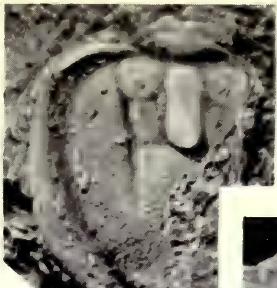
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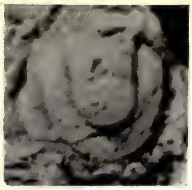
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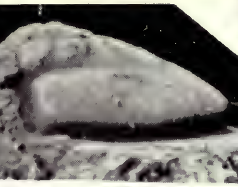
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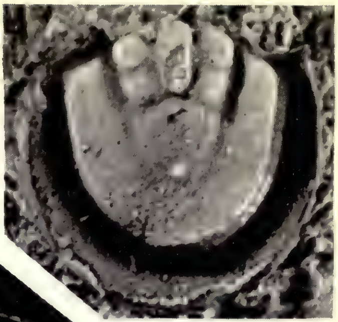
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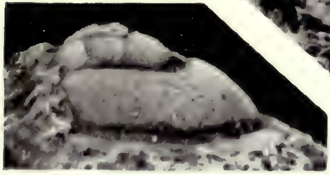
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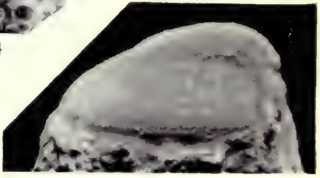
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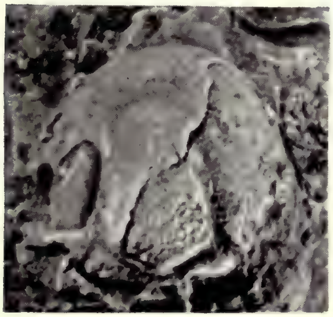
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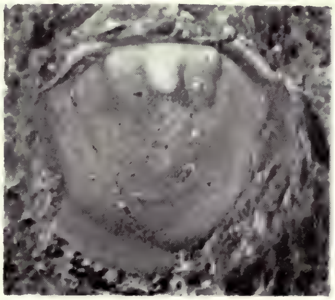
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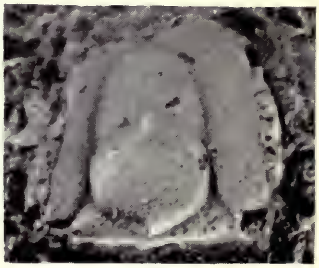
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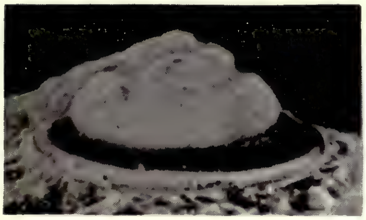
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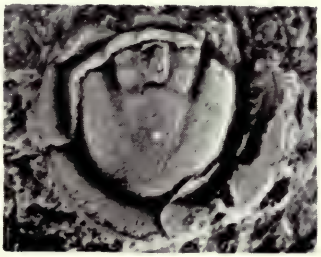
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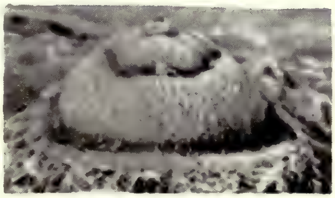
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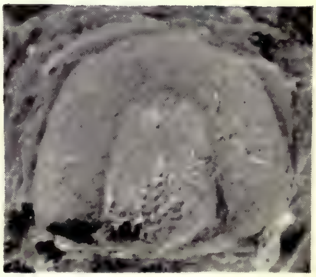
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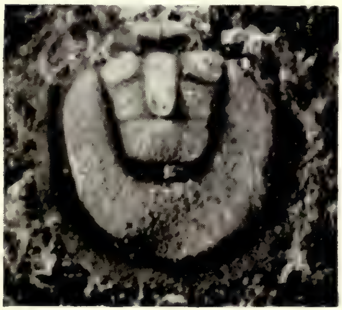
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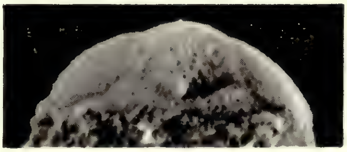
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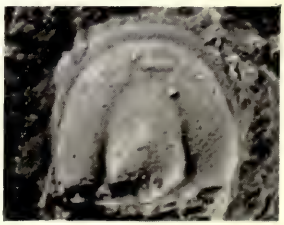
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PLATE 2

Ampyx sp. p. 291

Sobova Formation, locality B.651

FIGS. 1, 4, 7, 11. Anterior, plan, right anterolateral and left lateral views of cranidium lacking frontal spine. It.7897. × 6.

Trinucleid gen. et sp. indet. p. 293

Sobova Formation, locality B.651

FIGS. 2, 8. Latex cast and fragmentary internal mould of part of cephalic fringe. Note girder and one E arc of pits. It.7898a, b. × 10.

FIG. 6. Small fragment of fringe showing girder and possibly two arcs of E pits. It.7901. × 10.

Pliomerina sp. p. 294

Sobova Formation, locality C.429

FIGS. 3, 13. Internal mould and latex cast of incomplete glabella. It.7899a, b. × 7.

Cheirurid gen. et sp. undetermined p.294

Sobova Formation, locality B.651

FIG. 5. Latex cast of right librigena. It.7900. × 10.

Harpidid gen. et sp. indet. p. 292

Sobova Formation, locality C.429

FIG. 9. Latex cast of fragment of fringe showing marginal rim. It.7902. × 10.

Harpides sp. p. 292

Sobova Formation, locality B.651

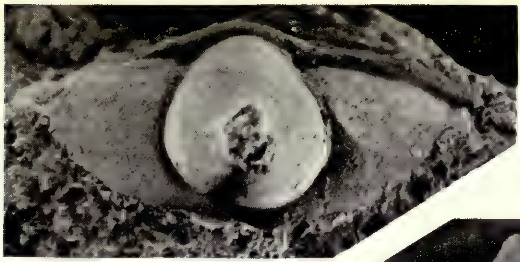
FIG. 10. Latex cast of fragment of cephalic fringe. It.7903. × 6.

FIG. 12. Fragment of fringe showing ventral surface and part of impression of dorsal surface. It.7904. × 7.

Apatokephalus sp. p. 302

Sobova Formation, locality B.651

FIG. 14. Fragment of right side of glabella. It.7915. × 10.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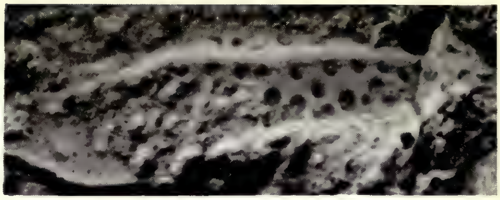
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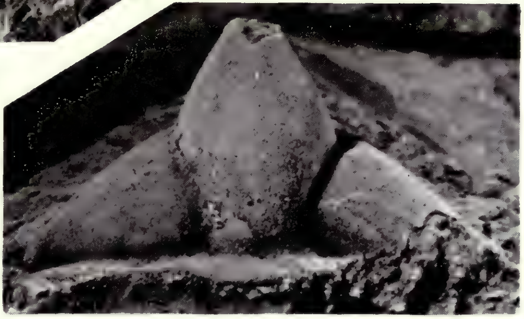
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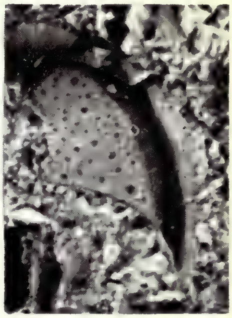
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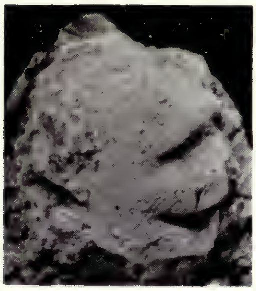
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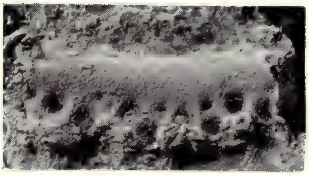
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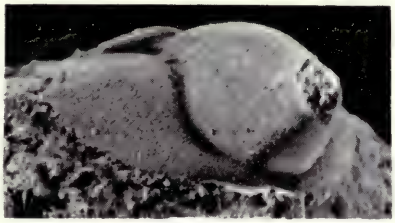
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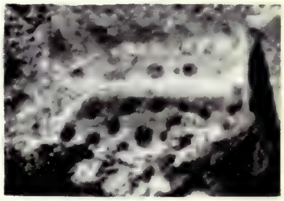
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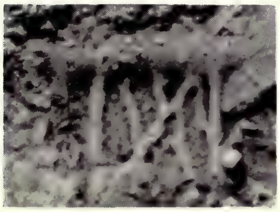
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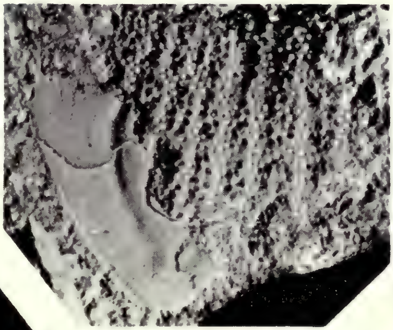
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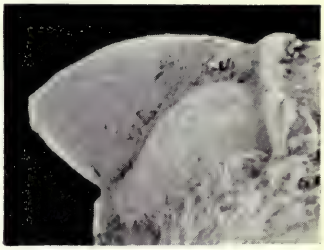
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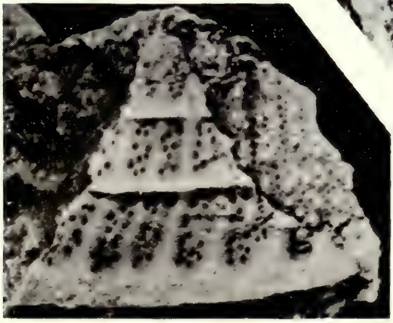
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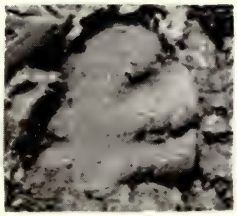
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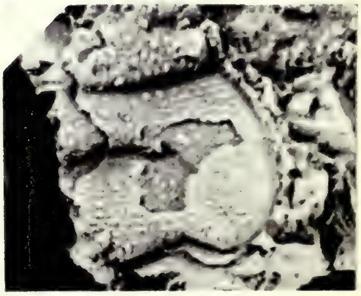
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PLATE 3

Pterygometopus ? sp. p. 295

Sobova Formation, locality B.651

FIGS. 1–3. Plan, left lateral and anterior views of internal mould of incomplete cranidium. It.7906. × 7.

FIGS. 7, 14. Plan views of latex cast and counterpart internal mould of incomplete pygidium. It.7912. Fig. 7, × 7; Fig. 14, × 6·5.

Carolinites sp. p. 300

Sobova Formation, locality B.651

FIGS. 4, 12, 13. Anterior, plan and right lateral views of incomplete, partly exfoliated cranidium. It.7907. × 6.

Euloma (Lateuloma) latigena subgen. et sp. nov. p. 297

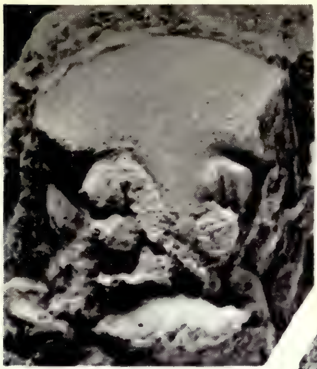
Sobova Formation, locality C.429

FIG. 5. External mould of incomplete pygidium. Paratype. It.7908. × 6.

FIGS. 6, 10, 11. Anterior, left lateral and plan views of partly exfoliated cranidium. Paratype. It.7909. × 4·5.

FIG. 8. Plan view of cranidium. Note eye-ridges and row of pits along anterior border furrow. Holotype. It.7910. × 6.

FIG. 9. Internal mould of cranidium. Paratype. It.7911. × 4.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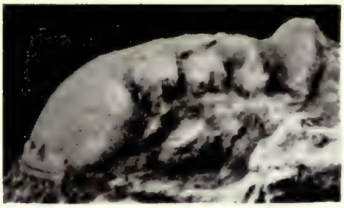
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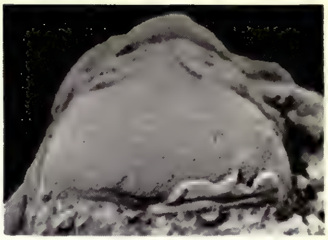
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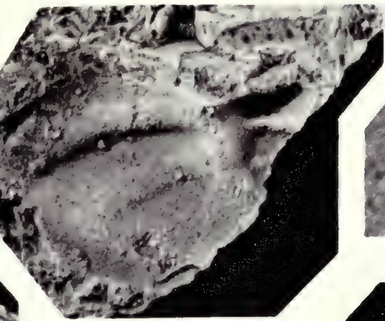
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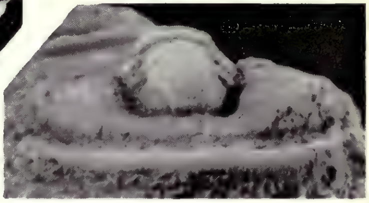
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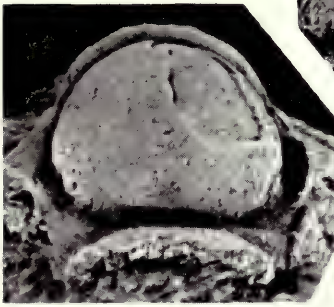
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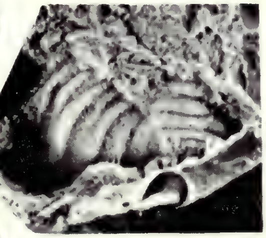
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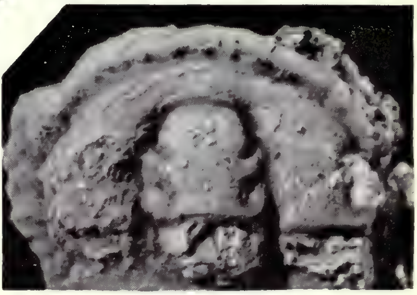
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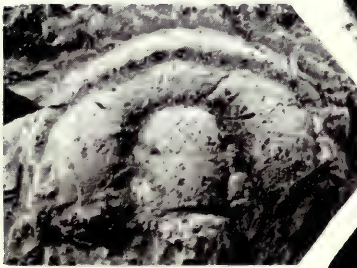
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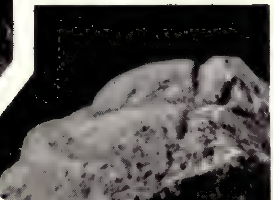
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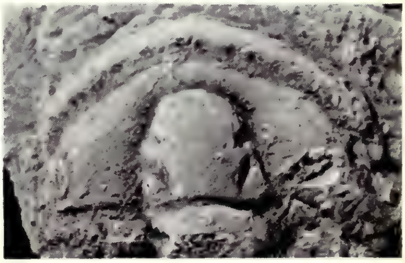
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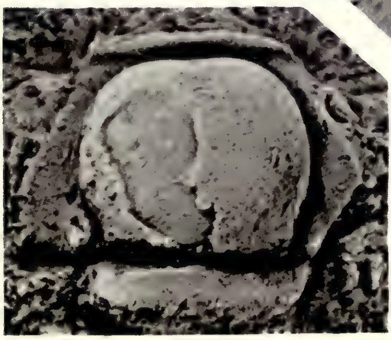
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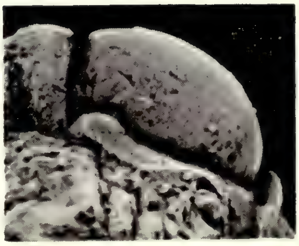
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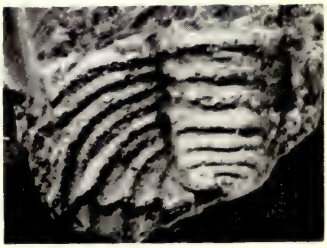
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PLATE 4

Agerina pamphylica sp. nov. p. 303

Sobova Formation, locality B.651

FIG. 1. Internal mould of two incomplete cranidia. Left-hand specimen only listed in Table of Dimensions. Paratype. It.7913. × 8.

FIG. 2. Internal mould of incomplete cranidium showing position of palpebral lobe and glabellar furrows. Holotype. It.7914. × 10.

FIG. 4. Latex cast showing pitting of surface of glabella and fixigenae. Paratype. It.7916. × 10.

FIG. 5. Plan view of pygidium showing marginal terrace-lines. Paratype. It.7917. × 12.

FIG. 6. Plan view of partly exfoliated pygidium. Paratype. It.7918. × 10.

Sobovaspis tuberculata gen. et sp. nov. p. 307

Sobova Formation, locality B.651

FIG. 3. Incomplete left librigena. Paratype. It.7924. × 6.

FIGS. 8, 11, 13. Plan, left lateral and anterior views of fragmentary cranidium. Note large tubercles on glabellar surface. Holotype. It.7920. × 4.

FIG. 10. Fragment of internal mould of cranidium showing position of left palpebral lobe. Paratype. It.7922. × 5.

FIGS. 12, 14, 15. Right anterolateral, plan and frontal views of incomplete cranidium. Paratype. It.7923. × 6.

Apatokephalus sp. p. 302

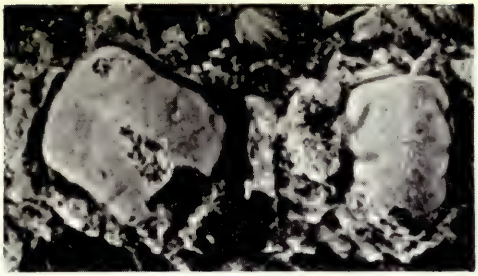
Sobova Formation, locality B.651

FIG. 7. Incomplete left librigena. Note longitudinal ridges and genal notch. It.7919. × 5.

Agerina ? sp. p. 305

Sobova Formation, locality B.651

FIG. 9. Plan view of small pygidium. Note pitted surface, raised rim and axis extending to tip of pygidium. It.7921. × 10.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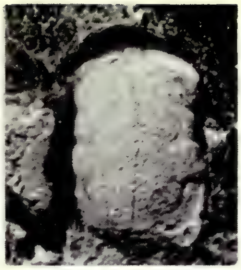
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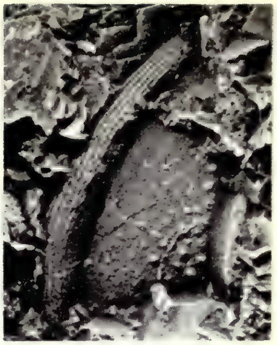
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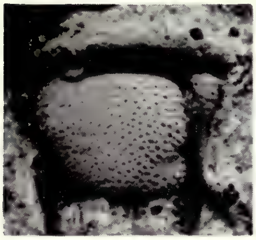
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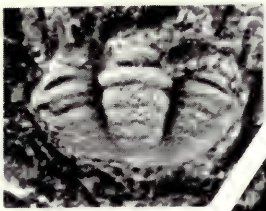
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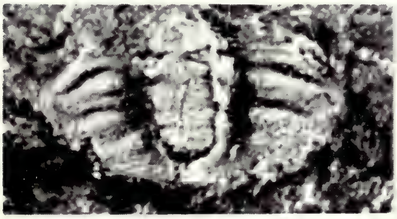
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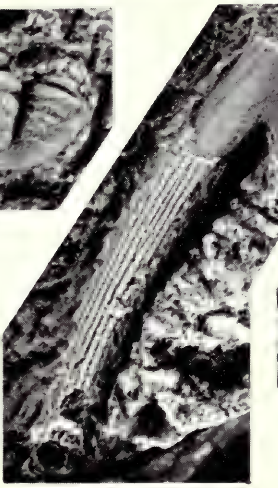
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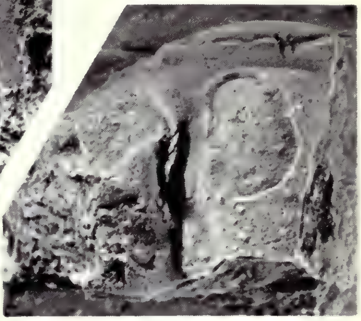
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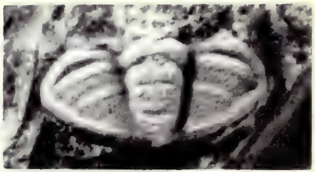
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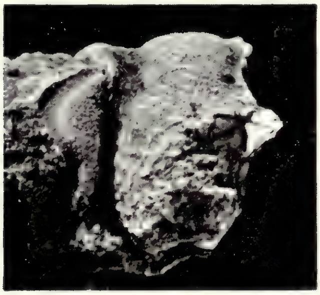
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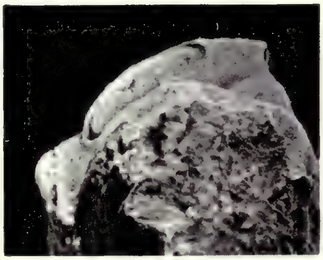
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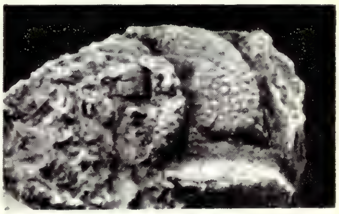
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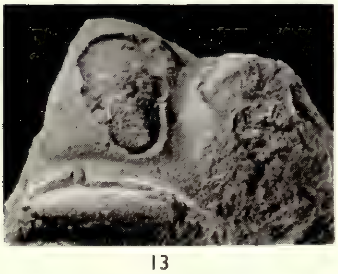
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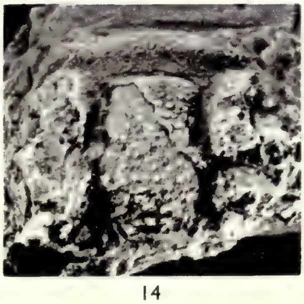
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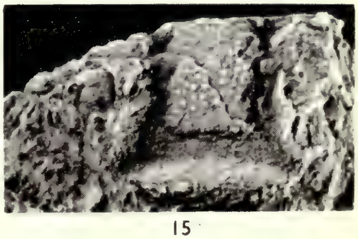
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PLATE 5

Metopolichas sp. p. 312

Sobova Formation, locality B.651

Fig. 1. Fragment of external mould of exoskeleton showing closely grouped tubercles. It.7905. × 8.

Figs. 7, 12, 15. Plan, anterior and left lateral views of hypostoma. It.7929. × 6.

Fig. 8. Part of pygidial doublure with fragment of external mould of dorsal surface of same pygidium. It.7930. × 6.

Phillipsinella matutina sp. nov. p. 309

Sobova Formation, locality B.651

Figs. 2, 5, 10. Plan, right lateral and frontal views of incomplete, partly exfoliated cranidium. Paratype. It.7925. × 12.

Figs. 3, 9. Oblique left lateral and plan views of incomplete cranidium. Note small anterior border, shape of frontal glabellar lobe, and pitted surface. Holotype. It.7926. × 12.

Figs. 4, 11. Plan and left posterolateral views of incomplete pygidium. Paratype. It.7927. × 12.

Agerina pamphylica sp. nov. p. 303

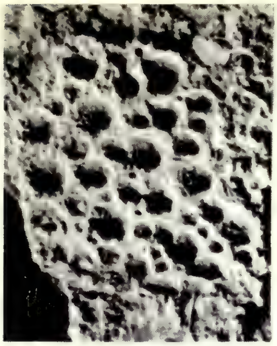
Sobova Formation, locality B.651

Fig. 6. Incomplete cranidium showing pitted exoskeleton and position of palpebral lobes. Paratype. It.7928. × 12.

Pseudopetigurus cf. ***hofmanni*** (Perner) p. 305

Sobova Formation, locality B.651

Figs. 13, 14, 16. Right lateral, plan and anterior views of incomplete cranidium. It.7931. × 4.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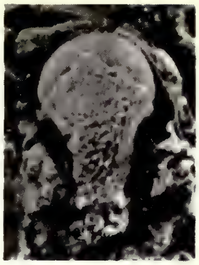
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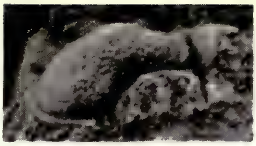
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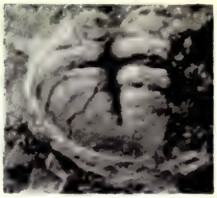
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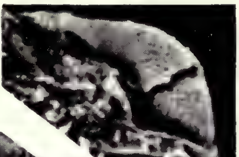
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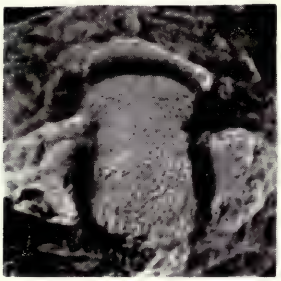
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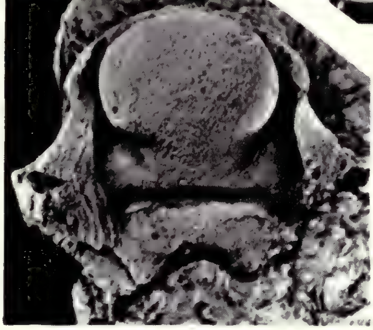
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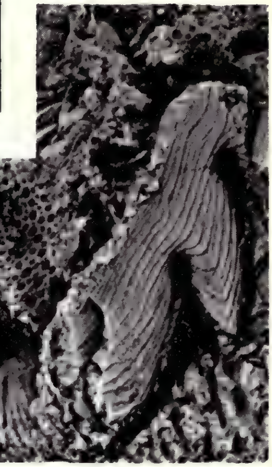
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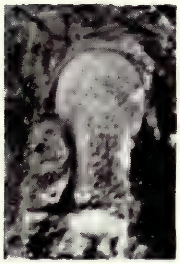
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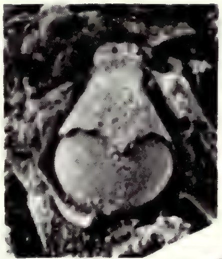
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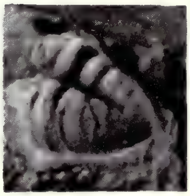
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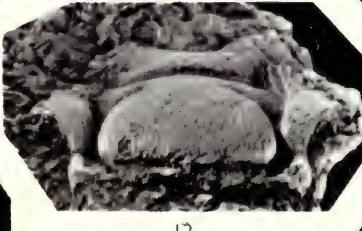
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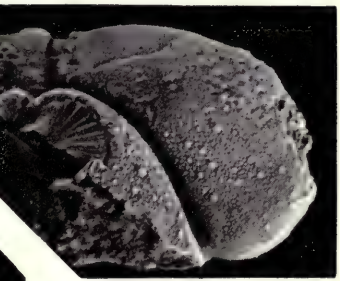
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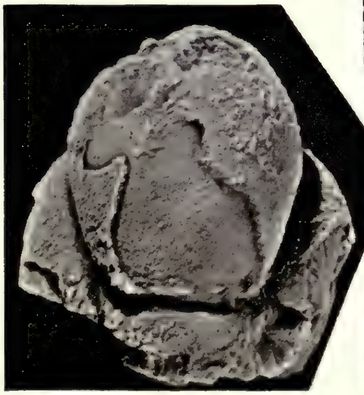
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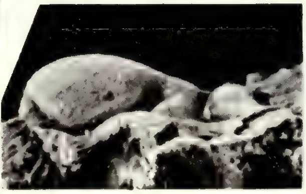
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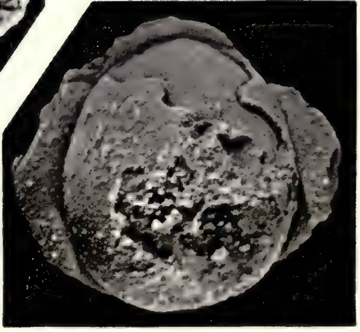
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PLATE 6

Metopolichas sp. p. 312

Sobova Formation, locality B.651

FIGS. 1, 5. Plan and right anterolateral views of fragmentary cranidium. It.7932. × 7.

FIG. 10. Almost complete hypostoma. It.7938. × 6.

FIG. 15. Plan view of hypostoma showing pitting of central lobes, and subconcentric ridges along border. It.7942. × 7.

Pricyclopyge superciliata sp. nov. p. 314

Sobova Formation, locality C.429

FIGS. 2, 6, 8. Anterior, plan and left lateral views of almost exfoliated cranidium. Holotype. It.7933. × 7.

FIG. 4. Lateral view of left eye. Paratype. It.7935. × 8.

FIG. 9. Part of right eye and librigena. Paratype. It.7937. × 8.

FIG. 14. Plan view of small cranidium. Note basal glabellar lobes. Paratype. It.7941. × 8.

Cyclopygid ? genus and species undetermined p. 316

Sobova Formation, locality B.651

FIG. 3. Plan view of almost exfoliated pygidium. It.7934. × 10.

Illaenus cf. ***herculeus*** Gortani p. 317

Sobova Formation, locality B.651

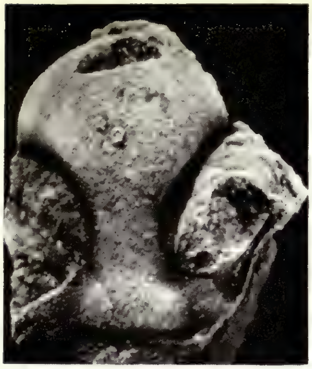
FIGS. 7, 11, 16. Anterior, right lateral and plan views of incomplete cranidium. It.7936. × 5.

FIG. 13. Latex cast of hypostoma. It.7940. × 7.

Illaenid genus and species undetermined p. 318

Sobova Formation, locality B.651

FIG. 12. Incomplete internal mould of small pygidium. It.7939. × 7.



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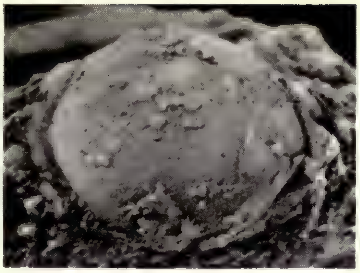

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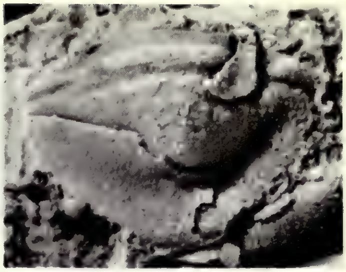

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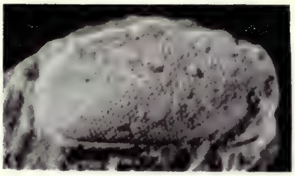

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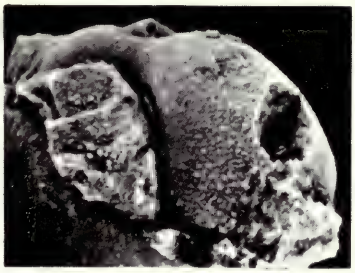

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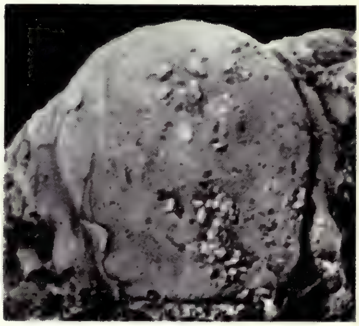

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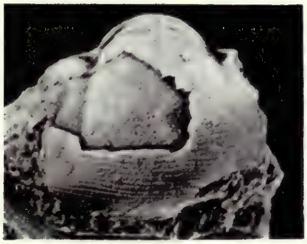

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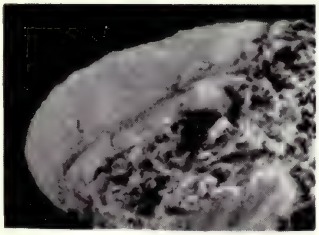

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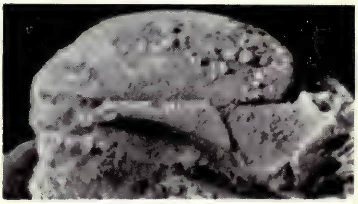

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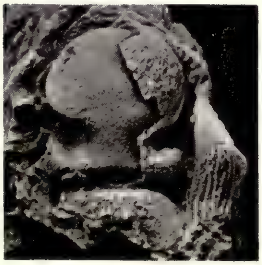

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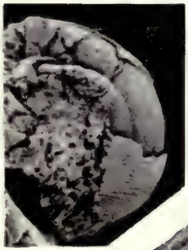

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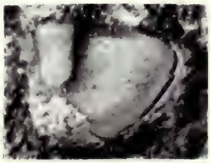

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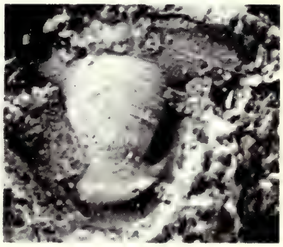

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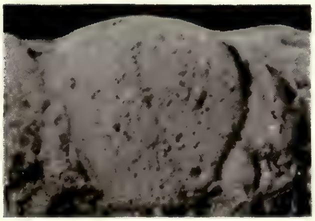

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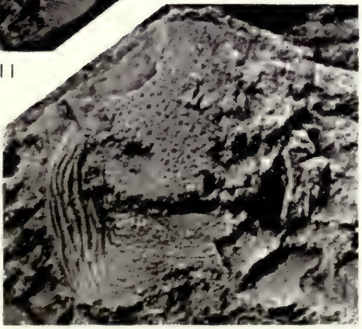

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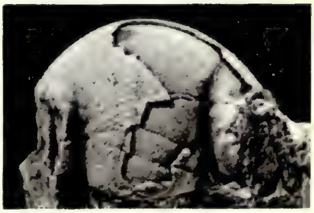

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PLATE 7

Protostygina sp. p. 316
Sobova Formation, locality B.651

FIGS. 1, 3, 5. Posterior, plan and left lateral views of partially exfoliated pygidium. It.7943. ×4. Fig. 10 = fragment of counterpart of same specimen. Note thin, low ridges on outer surface of exoskeleton and pitting of internal mould.

Genus and species undetermined A p. 335
Sobova Formation, locality B.651

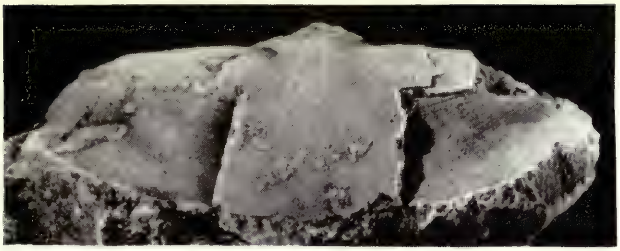
FIGS. 2, 4, 9. Plan, posterior and left lateral views of pygidium. It.7944. ×9.

Illaenus cf. ***herculeus*** Gortani p. 317
Sobova Formation, locality B.651

FIGS. 6, 7, 13. Plan, anterior and right lateral views of exfoliated cranidium. It.7945. ×7.
FIGS. 8, 11, 14. Left lateral, anterior and plan views of cranidium. It.7946. ×2.

Illaenid genus and species undetermined p. 318
Sobova Formation, locality B.651

FIG. 12. Plan view of pygidium. Note small, narrow axis. It.7947. ×5.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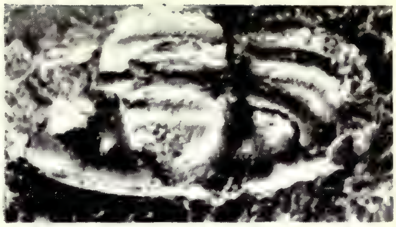
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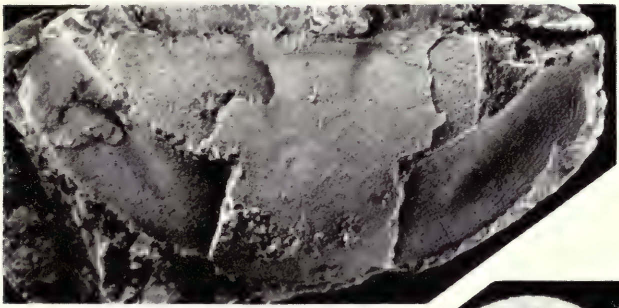
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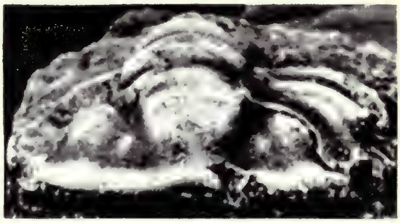
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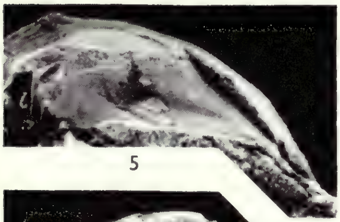
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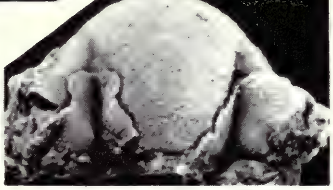
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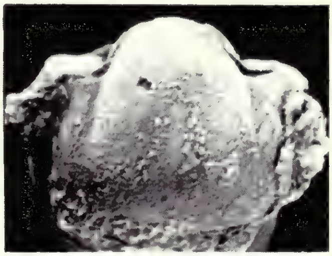
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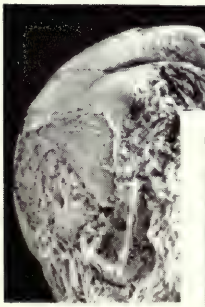
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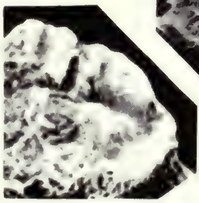
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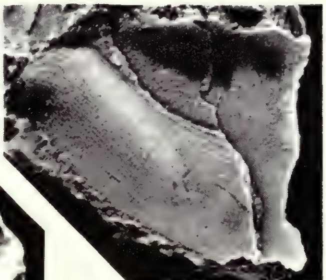
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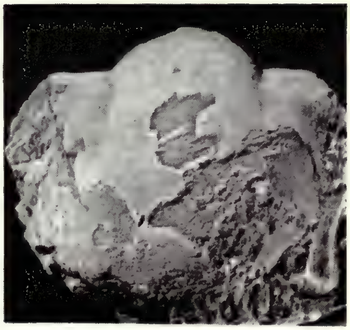
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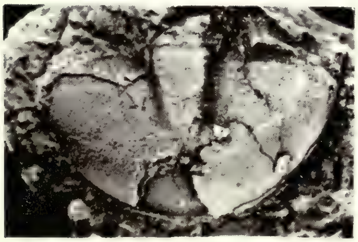
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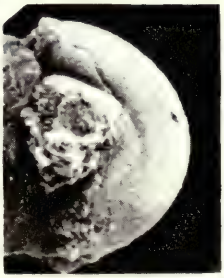
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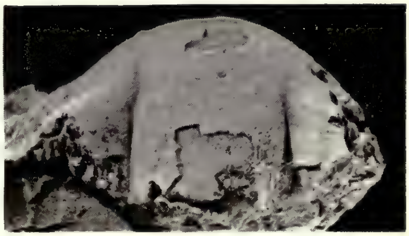
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PLATE 8

Symphysurus pannuceus sp. nov. p. 325

Sobova Formation, locality B.651

FIG. 1. Internal mould of hypostoma questionably referred to this species. It.7948. × 4.

FIGS. 4–6. Anterior, right lateral and plan views of almost exfoliated cranidium. Paratype. It.7950. × 2.

FIG. 7. Internal mould of incomplete pygidium. Note closely grouped small pits on surface of internal mould. Paratype. It.7951. × 3.

FIG. 11. Large pygidium showing fragment of outer surface, part of internal mould, and external mould of ventral surface of doublure with terrace-lines. Paratype. It.7953. × 3.

FIG. 12. Incomplete pygidium showing internal mould of dorsal exoskeleton and fragment of doublure. Paratype. It.7954. × 3.

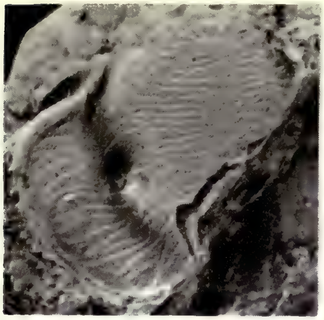
FIG. 13. Latex cast of right anterolateral portion of glabella to show ornamentation of subconcentric ridges. Paratype. It.7955. × 3.

Nileus sp. p. 323

Sobova Formation, locality C.429

FIGS. 2, 3, 10. Anterior, plan and left lateral views of incomplete cranidium. It.7949. × 4.

FIGS. 8, 9, 14. Right lateral, plan and anterior views of internal mould of incomplete cranidium. It.7952. × 4.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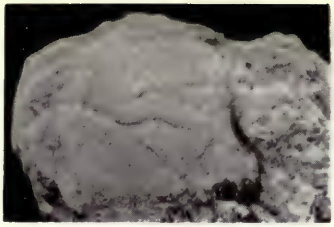
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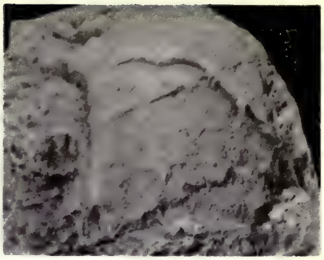
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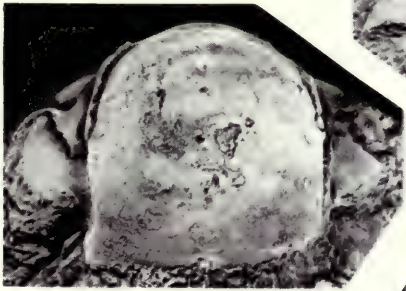
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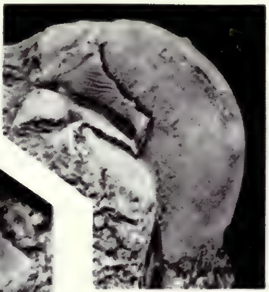
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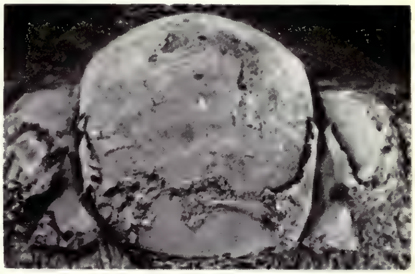
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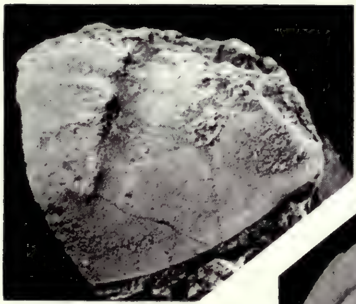
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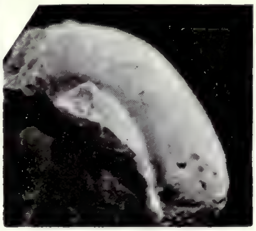
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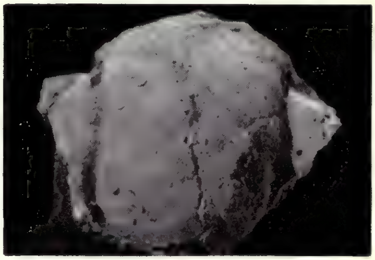
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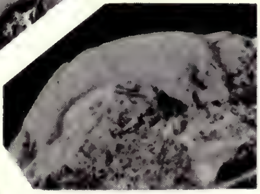
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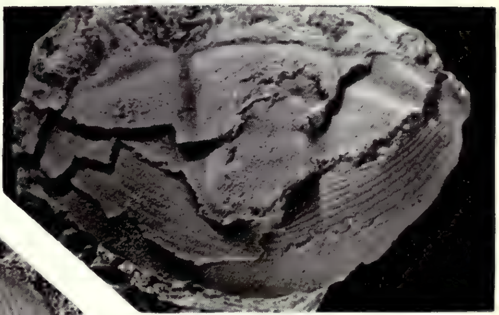
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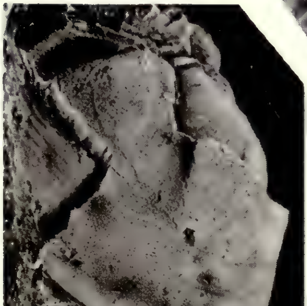
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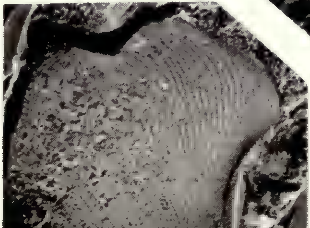
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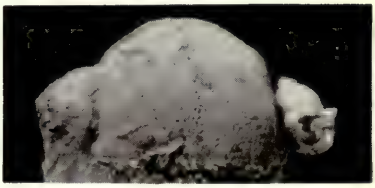
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PLATE 9

Symphysurus sp. p. 328
Sobova Formation, locality C.429

Fig. 1. Plan view of pygidium. It.7956. × 5.

Panderia monodi sp. nov. p. 320
Sobova Formation, locality B.651

Figs. 2, 3, 7. Plan, anterior and left lateral views of partly exfoliated, incomplete cranidium. Paratype. It.7957. × 3.

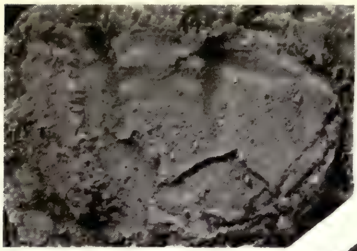
Figs. 4, 8, 9. Left lateral, plan and anterior views of internal mould of cranidium. Note axial furrows, palpebral lobes, anterior border and facial suture. Holotype. It.7958. Figs. 4, 8, × 5; Fig. 9, × 4·5.

Symphysurus pannuceus sp. nov. p. 325
Sobova Formation, locality B.651

Figs. 5, 10, 11. Plan, right lateral and thoracic views of enrolled individual. Holotype. It.7959. × 2·5. Fig. 12 = enlargement (× 4) to show facial suture, cephalic doublure and vincular notch in front of genal angle. See also Pl. 10, fig. 4.

Genus and species undetermined B p. 336
Sobova Formation, locality C.429

Fig. 6. Plan view of internal mould of pygidium. It.7960. × 7.



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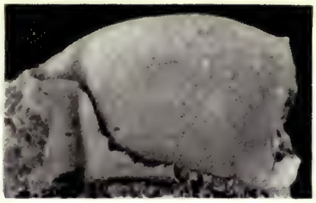

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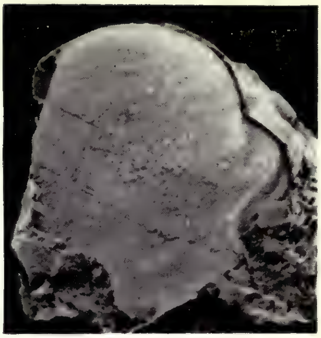

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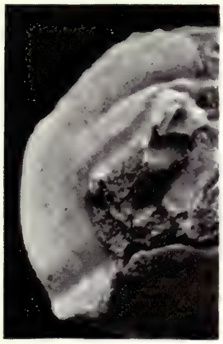

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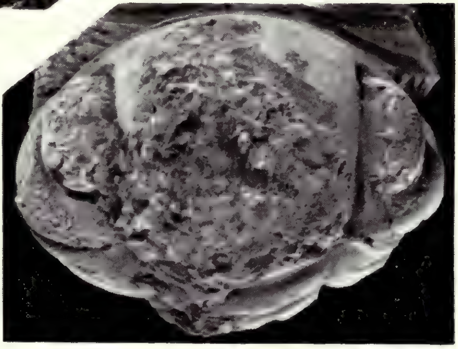

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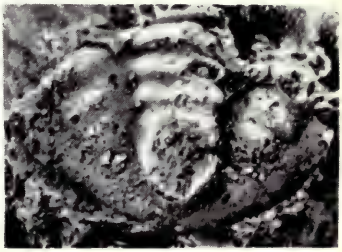

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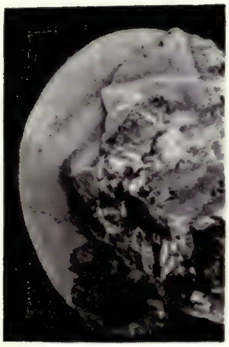

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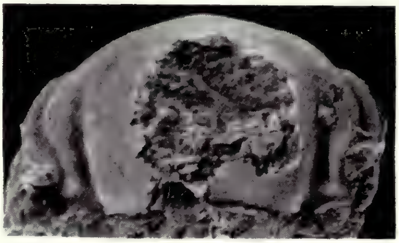

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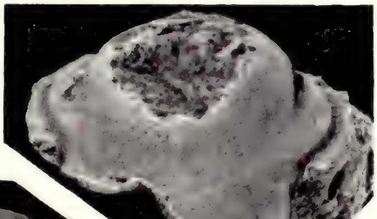

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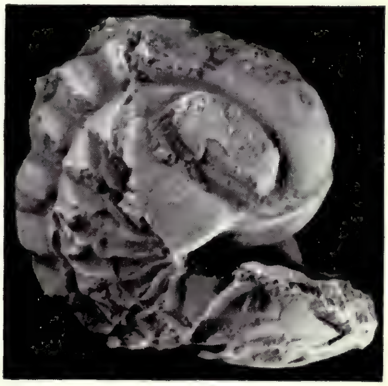

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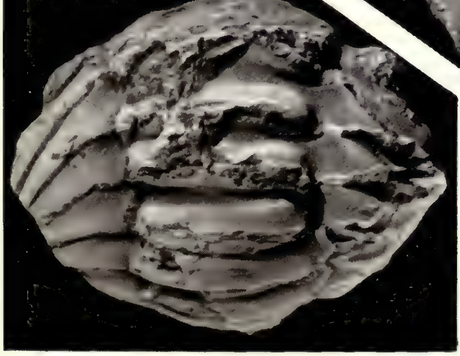

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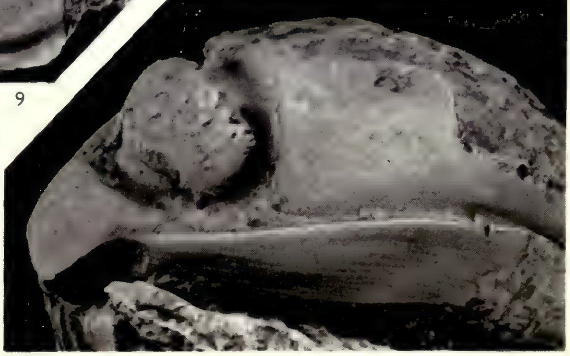

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PLATE 10

Niobe sobovana sp. nov. p. 330

Sobova Formation, locality B.651

Fig. 1. Close-up of right anterolateral portion of glabella to show ornamentation of ridges and pits (see description). Figs. 3, 10, 11. Anterior, plan and right lateral views of damaged cranidium. Holotype. It.7961. Fig. 1, ×6: others ×2.

Panderia monodi sp. nov. p. 320

Sobova Formation, locality B.651

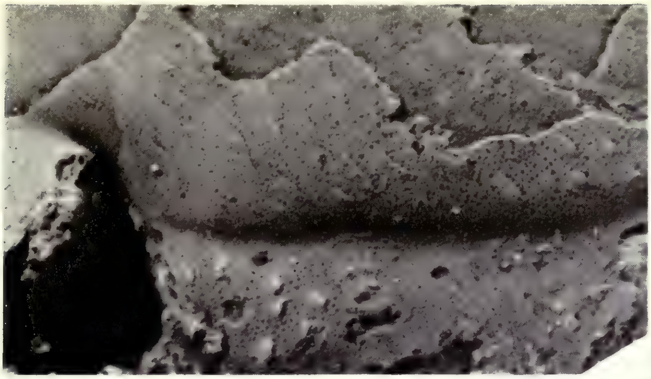
Figs. 2, 5, 6. Plan, left lateral and posterior views of internal mould of pygidium. Note furrow possibly coinciding with inner margin of doublure. Paratype. It.7962. ×3·5.

Figs. 7–9. Anterior, plan and left lateral views of cranidium. Paratype. It.7963. ×5.

Symphysurus pannuceus sp. nov. p. 325

Sobova Formation, locality B.651

Fig. 4. Plan view of pygidium and part of thorax. Holotype. It.7959. ×2·5. See also Pl. 9, figs. 5, 10–12.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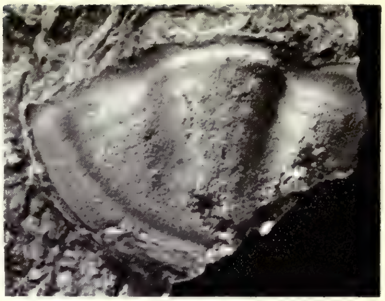
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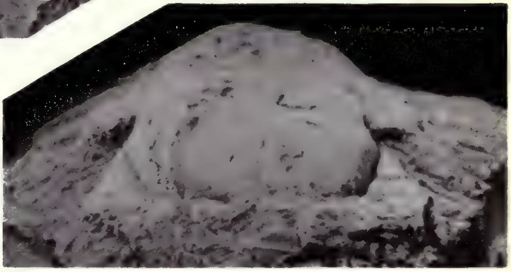
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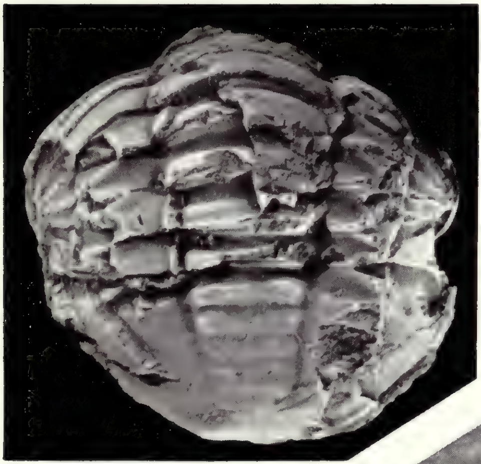
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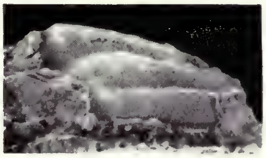
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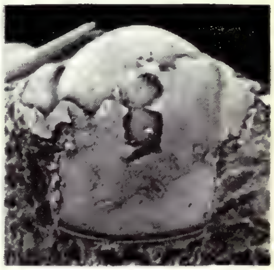
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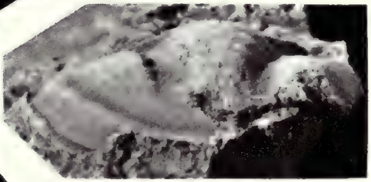
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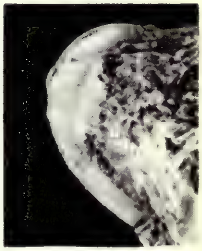
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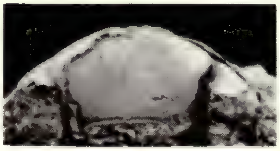
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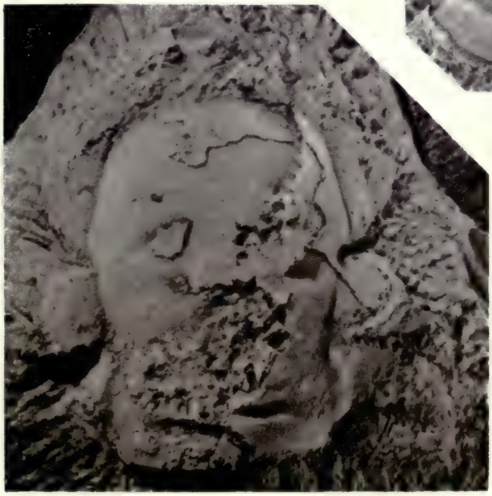
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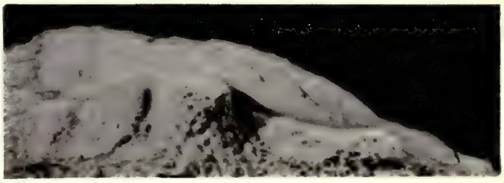
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PLATE 11

Niobe sobovana sp. nov. p. 330
Sobova Formation, locality B.651

FIG. 1. Latex cast of left librigena. Paratype. It.7964. × 2·5.

FIGS. 3, 6. Latex cast and internal mould of hypostoma. Paratype. It.7966. × 4.

FIG. 5. Internal mould of incomplete large hypostoma. Paratype. It.7968. × 4.

FIG. 9. Fragment of pygidium with external mould of doublure. Paratype. It.7971. × 3.

Asaphid gen. et sp. undetermined p. 334
Sobova Formation, locality B.651

FIG. 2. Latex cast of hypostoma. It.7965. × 5.

FIG. 10. Left pleura of thoracic segment showing ornamentation of doublure. It.7972. × 2·5.

Sobova Formation, locality C.429

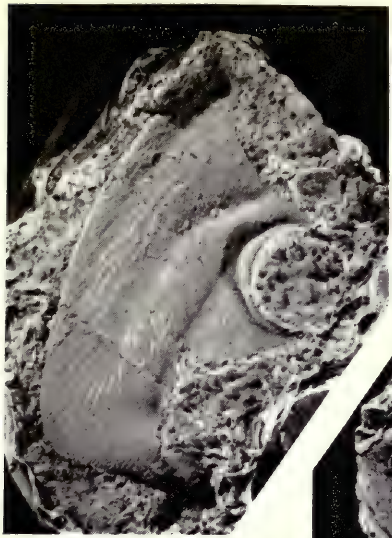
FIG. 8. Internal mould of hypostoma. It.7970. × 8.

Niobe ? sp. p. 333
Sobova Formation, locality B.651

FIG. 4. Plan view of pygidium with part of exoskeleton preserved. It.7967. × 4.

Nileus sp. p. 323
Sobova Formation, locality C.429

FIG. 7. Internal mould of hypostoma. Paratype. It.7969. × 4.



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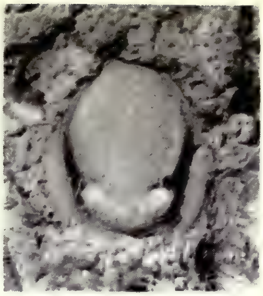

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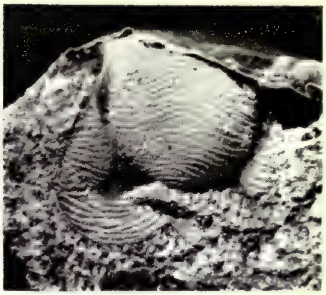

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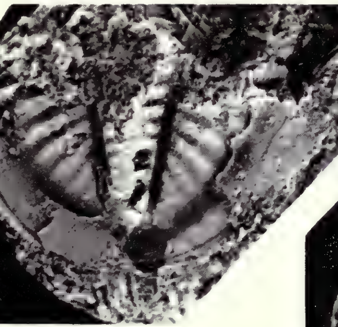

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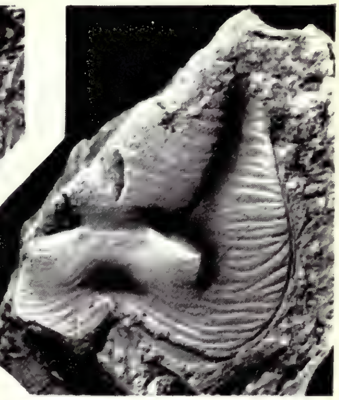

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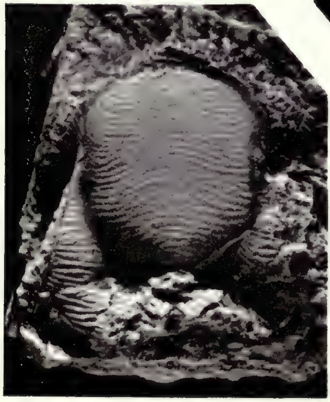

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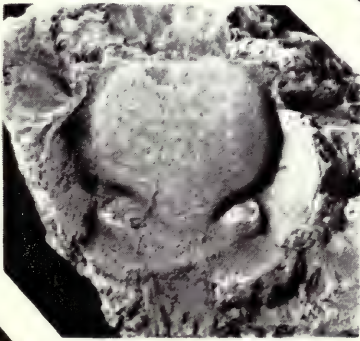

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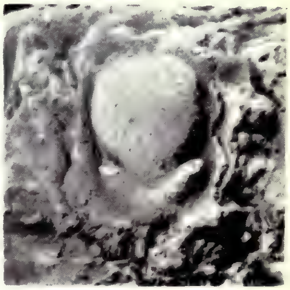

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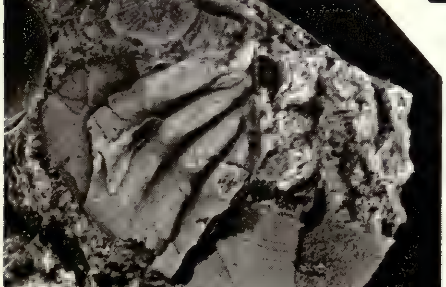

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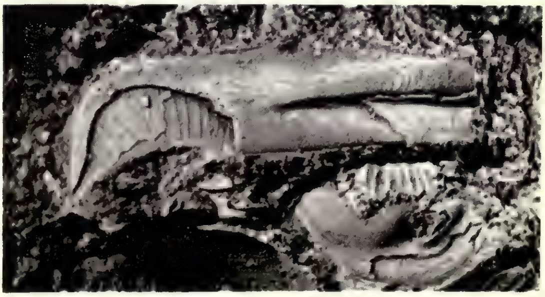

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PLATE 12

Ptychopyge elegans sp. nov. p. 329

Sobova Formation, locality B.651

FIGS. 1, 10, 12. Plan, left lateral and anterior views of internal mould of cranidium. Fig. 11 = latex cast of same specimen. Note longitudinal median ridge. Holotype. It.7973. × 4.

FIG. 2. Incomplete small cranidium. Paratype. It.7974. × 5.

FIG. 3 ?. Incomplete hypostoma referred questionably to this species. It.7975. × 6.

Symphysurus pannuceus sp. nov. p. 325

Sobova Formation, locality B.651

FIG. 4. Incomplete thoracic segment showing ornamentation of ridges on axial ring. Paratype. It.7976. × 4.

Asaphid gen. et sp. undetermined p. 334

Sobova Formation, locality B.651

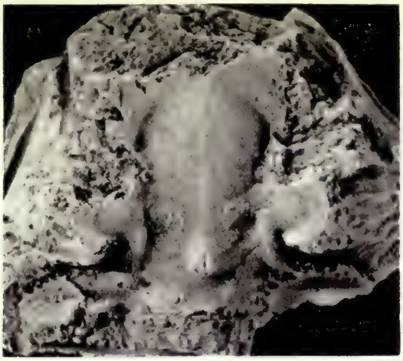
FIG. 5. Latex cast of fragmentary thoracic segment. It.7977. × 3.

FIG. 6. Internal mould of immature pygidium. It.10660. × 7.

FIG. 8. Partly exfoliated Meraspis ? pygidium, Degree unknown. It.7980. × 7.

Sobova Formation, locality C.429

FIG. 7. Fragment of internal mould of large pygidium. Fig. 9 = latex cast of same specimen, together with part of doublure. It.7978. × 3.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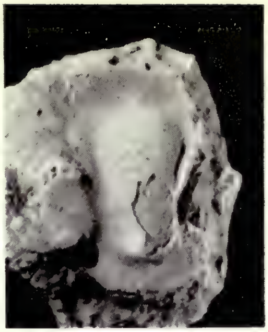
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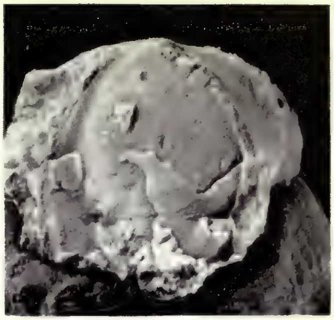
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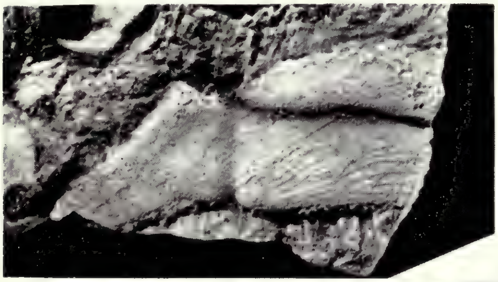
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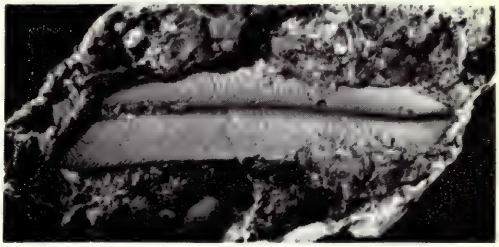
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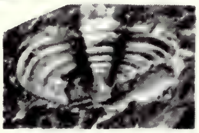
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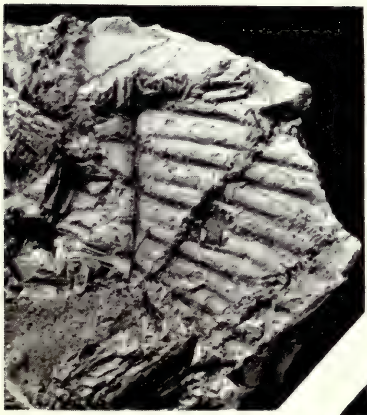
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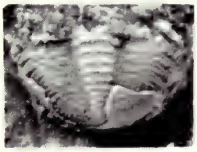
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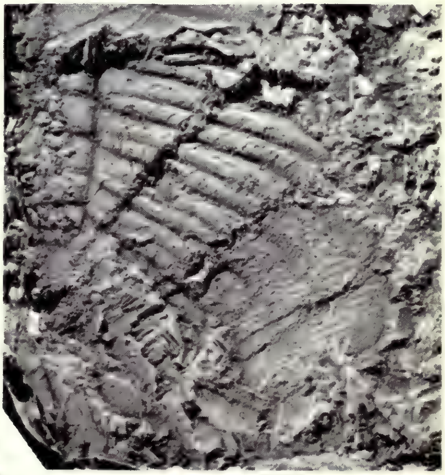
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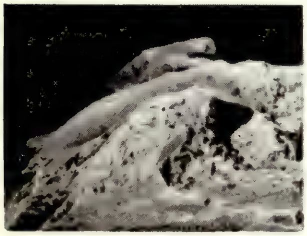
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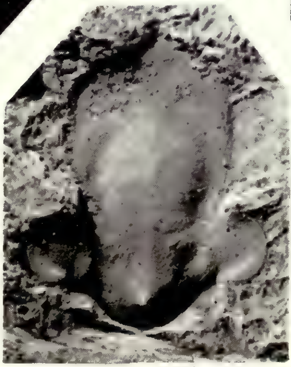
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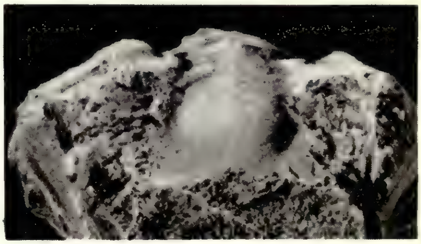
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WILLIAM ROGER HAMILTON

Pp. 349–395 ; 8 *Plates* ; 1 *Text figure*

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NORTH AFRICAN LOWER MIOCENE RHINOCEROSES

By W. R. HAMILTON

SYNOPSIS

The Lower Miocene locality of Gebel Zelten is probably of the same age and part of the same faunal unit as Moghara, Siwa and Wadi Faregh, Egypt. It has yielded the remains of two rhinoceroses – *Aceratherium campbelli* sp. nov. and *Brachypotherium snowi* (Fourtau). Remains of these species are described and compared with the East African early Miocene rhinoceroses, which they resemble more closely than the European rhinoceroses. The amount of described material of *B. snowi* is greatly increased and our knowledge of the North African Lower Miocene *Aceratherium* is expanded.

INTRODUCTION

THE discovery of fossil mammals at Gebel Zelten, Libya, was recorded by Arambourg and Magnier (1961) who collected in the area during 1960. Elements of the fauna were described in short notes by Arambourg (1961, 1961a, 1963). Collecting on a larger scale began in 1964 when Dr R. J. G. Savage first visited the area, and a preliminary note on this expedition (Savage & White 1965) contains a short faunal list which includes the rhinoceros *Brachypotherium*. Collecting in the area terminated in 1969. A large collection of fossil mammals from Gebel Zelten is now housed in Bristol University and at the British Museum (Natural History). Elements of the fauna described to date are – the ruminants (Hamilton 1973), *Megistotherium* (Savage 1973) and *Prodeinotherium* (Harris 1973). Studies of the anthracotheres, sirenians, gomphotheres, suids and carnivores are in preparation.

The geology of Gebel Zelten was described by Desio (1935), detailed sedimentological studies of the area were made by Selley (1966, 1967, 1969), and Doust (1968) studied the palaeoenvironment using invertebrate and trace fossils. The history of exploration, geography and geology of the area are summarized by Savage & Hamilton (1973).

The deposits at Gebel Zelten have been consistently dated as early Miocene by Arambourg (1961, 1961a, 1963), Savage (1967), Savage & White (1965) and Savage (in Selley 1969) refined the dating to early Lower Miocene. A faunal list for Gebel Zelten was given by Savage & Hamilton (1973). As Gebel Zelten and Moghara were probably part of the same faunal unit in early Miocene times, the faunal list for North Africa may be expanded by the inclusion of the Moghara, Siwa and Wadi Faregh faunas, resulting in a faunal list for the North African Lower Miocene sites which were probably also similar ecologically. The North African fauna agrees closely with the southern African sites, having three species in common with Muruarot (Madden 1972) and Rusinga (Bishop 1967) ; fairly close agreement with Bukwa (Walker 1969), and several genera in common with all three. Madden places

TABLE I

× agreement at specific level
○ agreement at generic level
a agreement at subfamily level

	ZELTEN	MOGHARA	SIWA	WADI FAREGH	CONGO	S.W. AFRICA	BUKWA	RUSINGA	MURUAROT	NAPAK	SONGHOR
Primates											
Prohylobates tandyi		×									
Cetacea											
Schizodelphis sulcatus		×	×	×							
Delphinus vanzerelli		×									
Sirenia indet	×										
Creodonta											
Megistotherium osteothlastes	×							?			
Anasinopa sp.	○							○	○		
Hyainailouros fourtaui		×						○		○	
Carnivora											
Afrocyon buroletti	×										
Amphycyoninae indet	a							a		a	a
Metailurus sp.	○							○			○
Proboscidea											
Gomphotherium spenceri		×	×								
G. angustidens	×	×		×	×		○	×	×	×	○
G. pygmaeus	×										
Prodeinotherium hobleyi	×				×		×	×	○		
Hyracoidea											
Saghatheriinae	a					a	a	a			
Perissodactyla											
Brachypotherium snowi	×	×	×		○	○		○	○	○	
Aceratherium campbelli	×	×			○			○	○	○	
Artiodactyla											
Brachyodus africanus		×	×	×							
Brachyodus sp.	○				○		○	○	○	○	
Hyoboops africanus	×						?	×			
H. moneyi	×	×									
Masritherium depereti		×									
Diamantohyus africanus	×					×	×		×		
Bunolistriodon massai	×							○	○		
Bunolistriodon sp. nov.	○										
Listriodon sp.	○				○		?				
Zarafa zelteni	×								○		
Prolibytherium magnieri	×										
Dorcatherium libiensis	×				○		○	○		○	○
Canthumeryx sirtensis	×								×		
Palaeomeryx sp.	○						○	○			
Gazella sp.	○										
Protragocerus sp.	○										
Eotragus sp.	○										

his Muruarot fauna in the early Miocene, using the figure of 18–22 million years given by Bishop, Miller & Fitch (1969) to define the limits of the lower Miocene in Africa. Napak is dated at 18–19 million years, Rusinga at about 19 million years, Songhor at 19·5–20 million years, and Bukwa at 22 million years (Bishop, Miller & Fitch 1969 p. 693). Bukwa (Mt Elgon) was independently dated at 22 million years by Brock & Macdonald (1969) and Rusinga at about 19·6 million years (VanCouvering & Miller 1969). Agreements at the specific and generic level between the North African faunas and the East African sites suggest that the North African sites may be aged between 19 and 22 million years.

Rhinoceroses were first described from the Lower Miocene of North Africa by Andrews (1900), who mentions an atlas vertebra which he assigns to an animal intermediate in size between *Aceratherium platyodon* and *Teleoceras* (= *Brachypotherium* here) *aurelianense*. Other specimens – an atlas and a scapula – were identified with *Aceratherium* sp. Fourtau (1918, 1920) described dental and postcranial material from Moghara which he assigned to the new species *Teleoceras* (= *Brachypotherium*) *snowi*, and additional material which he identified with the *Aceratherium* sp. of Andrews (1900). The presence of *B. snowi* at Gebel Zelten was recorded on faunal lists by Arambourg & Magnier (1961) and Arambourg (1963), and *Aceratherium* featured on faunal lists by Savage (1967, and in Selley 1969). An isolated M^3 from Siwa, Egypt, was identified with *B. snowi* by Hamilton (1973).

Rhinoceroses are well represented in Miocene deposits from Africa south of the Sahara, and Hooijer (1966) describes and figures four genera from East Africa of which three – *Dicerorhinus leakyi*, *Aceratherium acutirostratum* and *Brachypotherium heinzelini* – are represented by a large amount of well-preserved material. *Aceratherium acutirostratum* was originally described by Deraniyagala (1951a, b) as *Turkanatherium acutirostratus*, and the genus *Turkanatherium* features in a faunal list by Savage (1956). The same specimen was redescribed and figured by Deraniyagala (1953). Arambourg (1959) suggested that *Turkanatherium* might be a synonym of *Aceratherium*; this was supported by Hooijer (1963, 1966, 1968). There is a large amount of isolated material from East Africa which is assigned to *A. acutirostratum*, but the type skull is in Ceylon and I have not been able to see this specimen.

Dicerorhinus leakyi was described by Hooijer (1966) on the basis of an almost complete skeleton and much isolated material, some of which is in the collections of the British Museum (Natural History). Deraniyagala (1965) established the species *Aceratherium leakyi* based upon material which Hooijer (1963) had assigned to other species and which he later (Hooijer 1967) reidentified when establishing that the name *Aceratherium leakyi* was invalid.

Three genera and species of rhinoceroses – *Brachypotherium heinzelini*, *Aceratherium acutirostratum* and *Aceratherium cf. tetradactylum* – were described from the Lower Miocene of the Congo (Hooijer 1963). The material of *B. heinzelini* includes an astragalus which is undoubtedly brachypothere in features and several cheek teeth of which a left P^4 is the type of the species. A large number of specimens from East Africa have increased the knowledge of this species, which was redescribed in much more detail by Hooijer (1966). An isolated left M^2 and a fragment of a right upper molar were identified as *Aceratherium cf. tetradactylum* by Hooijer (1963), but the M^2 was reidentified as *Brachypotherium heinzelini* (Hooijer 1966) and the fragment also presumably belongs with this species, thus the record of *A. cf. tetradactylum* from Africa is not valid.

Stromer (1926) records the presence of Rhinocerotidae indet. in the Lower Miocene, South West African fauna. The specimen consists of a mandibular fragment containing P_4 to M_2, but this was not figured by Stromer. This specimen was described by Heissig (1971), who identifies it as *Brachypotherium heinzelini*.

Hooijer (1966) identified an isolated M^3 from Loperot and two isolated upper molar fragments from Rusinga as *Chilotherium*. However, he later (Hooijer 1971) reidentified these specimens with the new genus *Chilotheridium*, which he described from numerous specimens including two skulls and much post-cranial material. The Loperot site and other sites containing *Chilotheridium* are of differing ages. The specimens from Rusinga may be of early Miocene age, but the sites yielding these specimens – Gumba and Wakondu – are not yet definitely dated. The Bukwa II locality which has yielded fragmentary remains of *Chilotheridium* is about 22 million years, but Kirimum, Loperot and Ngorora are of late Miocene and early Pliocene age.

To summarize ; the early Miocene records of rhinoceroses from Africa south of the Sahara indicate the presence of four genera and species – *Aceratherium acutirostratum, Dicerorhinus leakyi, Brachypotherium heinzelini* and *Chilotheridium* ; the last not being specifically identified by Hooijer (1971) from the sites of early Miocene age. In Lower Miocene deposits in North Africa two rhinoceroses are recorded – *Aceratherium* and *Brachypotherium snowi*. None of the African early Miocene rhinoceros species is known outside Africa.

The classification and identification of the European rhinoceroses are confused, and in the following work I have attempted to use forms which are well defined and described. I have made extensive use of the collection of European rhinoceroses housed in the British Museum (Natural History), and I tried to use the same comparative specimens as were used by Hooijer (1966). In this way cross-reference with Hooijer's work may be simplified.

TERMINOLOGY

Anatomical terms used in this description are after Sisson & Grossman (1966) with the exception of the carpals and tarsals.

There is some controversy over the naming of the anterior teeth in rhinoceroses. The upper tusks are probably formed from the first upper incisors and this is generally accepted but the naming of the lower tusks is more difficult. Hooijer (1966) refers to these teeth as the canines but I have followed Radinsky (1969) who identifies them as the second incisors. In many forms, including at least one from Gebel Zelten, a pair of small incisors, probably the first, is present between the lower tusks.

Terms applied to the cheek teeth are after Osborn (1898) and Heissig (1969) and are demonstrated in text figure 1.

All the dimensions given in Tables 1–21 are measured in mm.

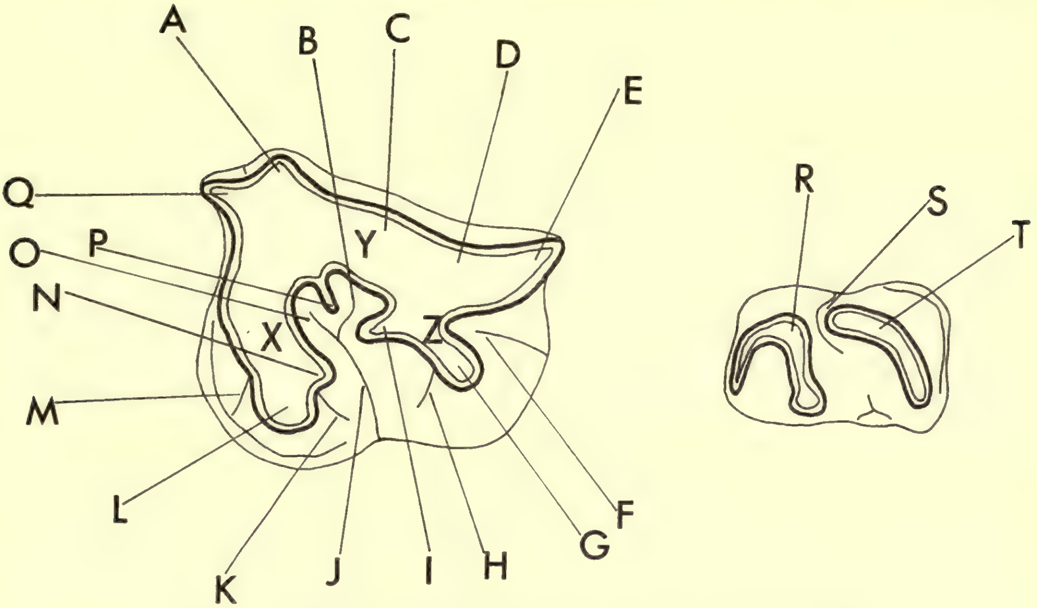

FIG. 1. Cusp nomenclature for the cheek teeth of rhinoceroses.
After Osborn (1898) and Heissig (1966).

A	Paracone
B	Medifossette
C	Mesostyle
D	Metacone
E	Metastyle
F	Postfossette
G	Hypocone
H	Hypocone groove
I	Crochet
J	Medisinus
K	Posterior protocone groove
L	Protocone
M	Anterior protocone groove
N	Antecrochet
O	Prefossette
P	Crista
Q	Parastyle
R	Metalophid
S	Labial groove
T	Hypolophid
X	Protoloph
Y	Ectoloph
Z	Metaloph

ABBREVIATIONS

Teeth are referred to by single capital letters – incisor (I), premolar (P), molar (M) and deciduous cheek tooth (D) – numbers are added above or below the line to define the tooth.

Specimens in institutions are referred to by: M., British Museum (Natural History), London; B.U., Department of Geology, University of Bristol; K.N., Centre for Prehistory and Palaeontology, Nairobi, Kenya. Recent material used was from the Department of Zoology, British Museum (Natural History) and is given the prefix M.O.

ACKNOWLEDGEMENTS

I would like to express my thanks to the people who have given assistance with this work. Dr R. J. G. Savage allowed me to study the material. Dr D. A. Hooijer provided information and comment. The plates were prepared by Miss T. Junker, Mr P. A. Richens and Mr T. W. Parmenter of the Photographic Unit, British Museum (Natural History). Dr R. C. Selley allowed me the use of his notes and

gave permission for the reproduction of two colour slides as plates and Mr A. R. Lindsay donated specimen M.29251.

SYSTEMATIC DESCRIPTIONS

Genus *ACERATHERIUM* Kaup 1832

DIAGNOSIS. Large, usually hornless rhinoceroses; I^1 and I_2 developed as tusks; upper molars with strong antecrochet; crochet usually strong; protocone constricted by anterior and posterior grooves; limbs long; feet four-toed.

COMMENTS. Although a predominantly hornless group, Osborn (1899) states that rudimentary horns may be present on the frontals. The post-cranial skeleton is virtually indistinguishable from that of *Dicerorhinus*. Metacarpal V is usually well developed whereas in *Dicerorhinus* it is usually small (Hooijer 1966), but this feature is of little use in identifying other post-cranial elements.

Aceratherium campbelli sp. nov.

DIAGNOSIS. A large species of *Aceratherium* in which the nasal notch is situated over P^2 and the facial region is long. The frontals are wide and a true sagittal crest is not developed. Supraoccipital region wide and vertical. Foramen ovale independent. Upper incisors well developed, P^1 large, cheek teeth high crowned. Length of cheek tooth row about 270 mm.

COMMENTS. This species is known only from North Africa, where it is well represented in the collections from Gebel Zelten and is also known from a few specimens from Moghara.

DERIVATION OF NAME. The trivial name is in honour of Dr A. Campbell of the Oasis Oil Company of Libya who provided much help and assistance during collecting expeditions to Gebel Zelten.

TYPE SPECIMEN. The skull (M.29250) which is almost complete but has poorly preserved cheek teeth (Pl. 1 & Pl. 2 fig. 3).

AGE AND LOCALITY. Lower Miocene. Gebel Zelten, Libya.

CRANIAL MATERIAL.

M.29250	: an adult skull in which the cheek teeth are poorly preserved and surface detail is difficult to see.
M.29251	: a pair of isolated nasals; donated by Mr A. R. Lindsay.
M.29252	: fragments of a shattered skull; cheek teeth; premaxillae and upper incisors.
M.29254	: a complete, isolated M^3.
M.29255	: a badly broken, isolated M^3 which agrees closely with M.29254.
M.29256	: the isolated lingual region of an M^2.
M.29257	: an isolated P_4 exhibiting medium wear.
M.29258	: an unerupted, isolated M_3.
M.29259	: a mandibular fragment with P_2–M_1 (P_4 only partly erupted) and fragments of M_2.
M.29266	: an isolated upper incisor which possibly belongs with *Aceratherium*.

M.29267 : labial fragments of P^3 and P^4, and the lingual region of P^3 : all from the uncollected skull (Pl. 3).

B.U.22925 : an almost complete left mandible with the posterior half of an unerupted M_3 and alveoli of P_1–M_3 preserved.

DESCRIPTION.

The skull. The sutures are completely closed on the skull (M.29250), and regions rather than individual bones are described. Much of the bone surface is coated with a ferrous concretion which is difficult or impossible to remove without seriously damaging the bone. The tips of the premaxillae, left wall of the cranium and crowns of most of the teeth are missing; the nasals are broken off and their junction with the rest of the skull is not preserved. Isolated elements are used to amend the description and were identified by comparison with the skull wherever possible. M.29252 was a complete skull, but it was badly shattered during transport to England. The cheek teeth are broken and fragmented, preserved parts agree with those of M.29250 but are more lightly worn. The premaxillae and upper incisors are preserved (Pl. 4 fig. 1).

An almost complete rhinocerotid skull was discovered near Transportation Corner, Gebel Zelten (Savage & Hamilton 1973), by Dr R. C. Selley while he was carrying out sedimentological studies in the area. Selley photographed the skull and made brief notes but having no equipment suitable for the recovery of such a large specimen he was forced to leave it. The skull was not found again but tooth fragments M.29267 from site 15 (Savage & Hamilton 1973, text fig. 3) – field number 6415.16 – agree closely in size and state of wear with those photographed (Pl. 3) and a white concretion present on the labial fragments is similarly distributed on the labial faces of the photographed specimen. This agreement leaves little doubt that fragments M.29267 are from the skull which was presumably broken up for souvenirs by oil workers in the area. The skull is the best recorded from Gebel Zelten as the tooth rows are complete, fragments of associated lower jaws are preserved and the premaxillae are attached. Photographs of this skull are reproduced here (Pl. 3 figs. 1 & 2) as they are the only complete record of this specimen and they were used in the interpretation of the less complete material which was returned to England. The dimensions of the skull and its lateral profile agree closely with the skull M.29250, thus confirming the identification of this specimen.

The skull: dorsal and facial regions. The distal regions of the premaxillae are missing in M.29250 and are described from M.29252. The bone is flattened transversely with convex lateral and plane medial faces. The bone surface of the lateral region is smooth but the medial face is heavily sculptured with numerous nutrient foramina. The dorsal edge is sharp and the ventral edge flattened with a shallow pit lying behind the I^1 alveolus; a similar pit is present on the skull (Pl. 3 fig. 1), in *A. incisivum* and in *D. schleiermacheri* a small I^2 is present in this region. The premaxilla becomes more flattened posteriorly, and the beginning of a ridge is preserved on the medial face of the left premaxilla. The proximal region of the premaxilla (M.29250) is shallow dorsoventrally, increasing in depth anteriorly and with a flattened medial region which reduces in width anteriorly. The bone curves ventrally and slightly laterally in front of the P^1 and is more slender but otherwise similar to that of *A. incisivum*. M.29250 and M.29252 have no regions of overlap, and the minimum length of the premaxillary region from the front of the P^1 was 130 mm ; this agrees with measurements from Pl. 3 and compares favourably with *A. incisivum* in which it is 160 mm.

The facial region is longer than in *A. incisivum* and lacks the preorbital concavity. The nasal notch is anteriorly situated, lying above the anterior edge of P^2 (Pl. 1 fig. 3) as in *D. sumatrensis* ; the notch is usually more posteriorly situated in aceratheres (Cooper 1934), lying over M^1 in *A. incisivum*, over P^4 in *A. tetradactylum* and *A. platyodon*, over P^3 in *A. lemanense* (Roman 1912 p. 63 fig. 19) and *A. acutirostratum* (Deraniyagala 1953 pl. 2 fig. b). The anterior border of the orbit is also anteriorly situated in M.29250, lying over the anterior end of M^1 whereas in *A. lemanense, A. platyodon, A. tetradactylum* and *A. acutirostratum* it lies over the anterior border of M^2, and in *A. incisivum* it lies over the middle of M^2.

The nasals of M.29250 are heavily encrusted and the bone surface is not visible ; the isolated nasal M.29251 was used to amend this description. The nasals curve slightly dorsally from the face of the frontals as in *A. incisivum*. Owing partly to the more anterior position of the nasal notch, the lateral region of the nasals is stronger and deeper in the Zelten form than in *A. incisivum* but compares in depth with the nasals of *A. lemanense* (Roman 1912 pl. 8 fig. 1a). The surface of the bone is roughened distally, and nasals M.29251 carry roughening half-way along their dorsal surfaces, this region is also produced as a weak eminence (Pl. 2 figs. 1 & 2), which is similarly positioned to that in *Chilotheridium pattersoni*. However, the eminence is much weaker than that of *Chilotheridium* (Hooijer 1971 pls. 4 & 5), but it carries a similar median groove and could represent an incipient stage in the development of a *Chilotheridium* type of nasals. It is possible that a small nasal horn was developed in *A. campbelli*, and the eminence is certainly as strong as that on the frontals of *A. incisivum* which Osborn (1899) used as evidence for the presence of a frontal horn.

The nasals are relatively stout and the median face of each is a plane, unsculptured, vertical wall except at the tips and in the postero-ventral region, where heavy sculpturing suggests close joining of the bones. The nasals of *A. incisivum* are about the same length as those of *A. campbelli* but in the latter the tips are flexed whereas in *A. incisivum* this flexion does not occur.

The frontals are wide in the supraorbital region (Pl. 1 fig. 1) and the dorsal region of the skull is similar in shape to *A. lemanense* (Roman 1912 pl. 8 fig. 1). A true sagittal crest is not formed in M.29250 but the temporal crests approach each other very closely (Pl. 1 fig. 1) ; a similar crest is formed in *A. lemanense* and in one of the skulls of *A. incisivum* (Kaup 1834 pl. 10 fig. 2a). In the other skull of *A. incisivum* (Kaup 1834 pl. 10 fig. 2b) and in *A. acutirostratum* (Hooijer 1966, p. 137) the temporal crests do not approach so closely. In lateral aspect the dorsal face of the skull is very concave (Pl. 1 fig. 3) owing to the great height of the occipital region. The occipital region is also high in *A. tetradactylum* (Wang 1928 p. 188 fig. 1a) and rises steeply from the frontal region of the skull in *A. acutirostratum* (Deraniyagala 1953 pl. 2 fig. 2b). The skull of *A. incisivum* rises steeply but the profile is less saddle-shaped and the skull of *A. lemanense* is uniformly low.

The zygomatic arch is wide and deep with a strong notch near its posterior end in the area dorsal to the ear region. The ear region is exposed laterally between the lateral edge of the nuchal crest and a ridge from the posterior end of the zygomatic arch (Pl. 1 fig. 3) ; this lateral exposure is similar in *A. acutirostratum* but it is wider in *A. lemanense* and *A. incisivum.* M.29250 has a very strong nuchal crest which extends laterally forming a posterior wall for the temporal fossa ; this does not occur in *A. incisivum, A. lemanense* or *A. acutirostratum* in which the nuchal crests are much narrower.

The skull : occipital and basicranial regions. The supraoccipital region is vertical in M.29250 as is usual in the aceratheres (Cooper 1934 p. 572). The dorsal region of the nuchal crest is not reflected, in contrast to *A. incisivum* and *A. lemanense* but in agreement with *A. acutirostratum.* Also in agreement with this species the occipital condyles are produced posteriorly to a greater extent than in *A. incisivum* or *A. lemanense.* The condyles are relatively large in M.29250 and in *A. acutirostratum* but are smaller in *A. incisivum* and *A. lemanense.*

In posterior aspect (Pl. 2 fig. 3) the occipital region differs in shape from the other aceratheres, mainly due to the great expansion of the nuchal crests. The supraoccipital region bears a deep median depression with a large tubercle and paired lateral depressions which are clearly defined by strong ridges above the condyles (Pl. 2 fig. 3). Unfortunately this region cannot be compared with that of *A. acutirostratum,* as the type skull of this species has undergone lateral compression and distortion. Ventrally the nuchal crest joins the post-tympanic process anterolateral to the condyles and from this the paroccipital process is produced : neither process is preserved but their bases suggest that the processes were relatively weak.

The basioccipital region is badly broken and is largely missing from M.29250 (Pl. 1 fig. 2). An anterior process was developed for the attachment of the rectus capitis ventralis muscle, and the post-tympanic process approaches the postglenoid process, but these regions do not fuse. The hypoglossal foramen is more anteriorly situated than in *R. unicornis, D. sumatrensis* or *A. incisivum* lying antero-medial to the base of the paroccipital process. The auditory region is exposed ventrally (Pl. 1 fig. 2) near the medial end of the paroccipital process and medial to it are two large foramina; one is probably the posterior lacerate foramen, and the lateral one is the stylomastoid foramen. Further details of the auditory region are obscured. The median lacerate foramen lies anterior to the auditory region. An important feature of the skull is the independent existence of the foramen ovale which lies anterior to the median lacerate foramen and slopes posterodorsally from its opening. The latter foramen is joined to the alisphenoid canal by a shallow groove, and a groove for an artery runs from its ventral edge into the ear region. The existence of an independent foramen ovale is unusual in rhinoceroses as the foramen lacerum medius and the foramen ovale are usually fused. However, Osborn (1898), with particular reference to the North American rhinoceroses, states that all degrees of fusion of the two foramina are demonstrated by the Oligocene and Miocene rhinoceroses, and an independent foramen ovale is known from *Chilotherium* (Edinger 1937 ; Edinger & Kitts 1954), though this is more posteriorly

TABLE 2

The skull of *Aceratherium campbelli*

	Aceratherium campbelli	*A. incisivum*	*A. acutirostratum*[1]	*A. lemanense*[2]	*Dicerorhinus leakyi*[3]
Length of skull. Occipital crest–tips of nasals	*c* 560–580	531	586	510	630
Width across postorbital processes	*c* 176	185	156	–	–
Maximum height of occiput	239	228	157	–	–
Depth of naso-maxillary notch from tip of premaxilla	–	270	–	–	145
Facial length from naso-maxillary notch to anterior edge of orbit	110	78	109	–	135
Length from front of orbit to posterior face of occipital condyles	355	389	329	–	–
Depth of skull and teeth at anterior edge of orbit	*c* 196	211	207	–	–
Width across zygomatic arches	380	345	320	–	–
Maximum width of occipital region	278	263	–	–	–

[1] After Deraniyagala 1951. [2] After Roman 1912. [3] After Hooijer 1966.

situated. The optic foramen opens immediately above the M^2. Between the foramen ovale and the optic foramen the bone is badly shattered, but the posterior opening of the alisphenoid canal is preserved and the foramen rotundum presumably opened into this canal.

In general features the skull of *A. campbelli* resembles that of *A. acutirostratum* more closely than any other acerathere, but it must be emphasized that this comparison and apparent resemblance are based upon published plates only. The anterior position of the orbit and nasal notch, form of the frontals, basicranial region and occiput serve to distinguish the skull of *A. campbelli* from that of *A. acutirostratum.*

Mandible. A nearly complete mandible of an almost adult individual (B.U.22025) is identified with *A. campbelli.* It is slightly smaller than those identified with *B. snowi* and the length of the cheek tooth row is about 240 mm which would rise to 250 mm in the fully adult condition ; this compares with an estimated length of 300 mm on mandible M.25126 which is identified with *B. snowi.* The mandible is shallow and similar in shape to that of *A. incisivum,* the ventral edge is slightly convex, and the leading edge of the vertical ramus rises steeply from the region of the partially erupted M_3 ; this leading edge is convex and relatively narrow. There are paired mental foramina with the larger lying below P_1. The symphysis starts in front of P_1 and was probably relatively short. The root of I_2 terminates in front of the P_1 in B.U.22025 and also in M.29259. The posterior half of the partially erupted M_3 is preserved ; this fragment indicates the presence of a strong labial groove which is a feature of the acerathere lower cheek teeth (Hooijer 1966), rather than of brachypothere teeth.

Upper dentition. The upper incisors of M.29252 are preserved (Pl. 4 fig. 1) ; they are almost complete and heavily worn. Hooijer (1966, p. 142) used the ratio of antero-posterior crown diameter to root length as a possible criterion by which the incisors of *Aceratherium* could be distinguished from those of *Brachypotherium.* On the I^1 of *Brachypotherium goldfussi* (Kaup 1854 : pl. 1 fig. 13) the antero-posterior crown diameter is greater than the root length, and in the I^1 of *B. brachypus* (M.33524) the crown length is 86 mm and the root length is not greater than 80 mm. This contrasts with the condition in the upper incisors of *A. incisivum* (Kaup 1834 pl. 14 figs. 1–3) in which the root length is always much greater than the crown length. The right upper incisor of M.29252 is the more complete and its root length exceeds the antero-posterior diameter of the crown (Table 3), which helps to confirm the identification of M.29252 as *Aceratherium* if Hooijer's criteria are valid. The crown of the incisor is heavily worn posteriorly but the anterior region is unworn (Pl. 4 fig. 1) ; this agrees with the wear pattern in *A. incisivum,* but differs from the wear in *D. sumatrensis* and *D. schleiermacheri* in which the whole crown of the tooth is worn uniformly.

An isolated, unerupted, right I^1 (M.29266) is smaller than those of M.29252. It has a long root (Pl. 4 fig. 6), and therefore cannot be identified with *Brachypotherium.* The tooth agrees closely with that of *A. incisivum* figured by Kaup (1834 pl. 14 fig. 7), but also agrees closely with that of *D. leakyi* (Hooijer 1966 pl. 4 fig. 7). The incisors of *A. incisivum* exhibit considerable variation in size and only a single individual of *A. campbelli* is represented by M.29252. M.29266 may thus simply represent a smaller individual of *A. campbelli,* or it may possibly indicate the presence of *Dicerorhinus* at Gebel Zelten.

Dentition : upper cheek teeth. The isolated upper cheek teeth and shattered upper dentitions of *Aceratherium* from Gebel Zelten have few corresponding parts preserved. This is unfortunate as it introduces some uncertainty into the grouping of these specimens. However, comparison of the material demonstrates that all the teeth fall into the same size range (Table 3), and features of the teeth are similar within the degree of variation usual in the rhinoceroses. The skull (M.29252) has a few upper teeth preserved and wherever possible these are used in the description to confirm the identification of isolated teeth.

A complete M^3 (M.29254) presents features characteristic of *Aceratherium.* The anterior cingulum is strong, giving way labially to a vertical depression on the face of the parastyle. The protocone constriction is strong with anterior and posterior grooves similar to *A. incisivum* and *A. lemanense,* but contrasting with *Dicerorhinus* in which the grooves are not present and the constriction consists of an anterior depression only. A hypocone groove is not present on either of the upper third molars. Immediately labial to the posterior protocone groove the antecrochet bulges basally extending across the medisinus ; this contrasts with *Dicerorhinus* (Hooijer 1966 p. 139). The parastyle is strong and narrow antero-posteriorly. The paracone swelling is very feeble, increasing in strength basally but is much weaker than in *D. leakyi, D. sumatrensis, A. incisivum* or *A. lemanense* ; as a result the posterior face of the tooth is convex (Pl. 4 fig. 3) whereas in the other species it carries a shallow labial concavity. The crochet is strong (Pl. 4 fig. 5), reducing basally. The presence of a crochet in M.29255 is indicated by a fold of the enamel face in the medisinus ; a crochet is present in *A. incisivum, A. lemanense* and *A. acutirostratum.* The medisinus is wide lingually (Pl. 4 fig. 3), and lacks a tubercle at its lingual end. A small postero-lingual cingulum is present and a weak posterior cingulum ; lingual cingula are present in *A. lemanense* and *A. incisivum* but their presence and strength are variable.

The lingual region of the M^1 has a strong anterior cingulum as in the M^3 ; the protocone is strongly constricted in M.29252 (Pl. 5 fig. 1), on the skull (M.29250 : Pl. 1 fig. 2), on the uncollected skull (Pl. 3), and on the M^2 fragment (M.29256 : Pl. 4 fig. 2). This is as in *A. lemanense, A. incisivum* and *A. acutirostratum,* but is in contrast to *Dicerorhinus.* A weak hypocone groove is also present on M.29252 and M.29256 as is usual when the protocone is strongly constricted (Hooijer 1968), but in contrast to the M^3. The antecrochet increases in strength basally, extending across the medisinus as in the M^3 and the other aceratheres, but in contrast to *Dicerorhinus.* The crochet is strong as in the M^3 but is more labially situated and is flexed more labially. The medisinus is open as in the M^3 and lacks a tubercle at the lingual end in M.29256 and M.29250 ; this region is not preserved in M.29252. The postero-lingual cingulum is strong and continues with the postfossette, but there is no extension of either posterior or anterior cingula onto the lingual region of the tooth ; this contrasts with *A. incisivum* and *A. lemanense* in which the cingula may extend onto the lingual face but do not usually join lingually. The labial region of M^1 is preserved on M.29252 ; the parastyle is weaker and the paracone relatively stronger than in *A. lemanense* (M.29264) as a result the antero-labial corner of the M^1 slopes more sharply lingually than is usual in the aceratheres. The labial face is shallowly concave and smoothly curved with a weak postero-labial cingulum and the posterior corner is sharp.

The P^4 (M.29252 : Pl. 5 fig. 1) exhibits medium wear and is almost complete ; a very heavily worn but nearly complete P^4 is preserved on the skull (M.29250 : Pl. 1 fig. 2) and the labial face of the P^4 (M.29267) is preserved from the uncollected skull (Pl. 3) ; this demonstrates that the tooth was very high. P^4 has a weaker protocone constriction than on the molars and the anterior protocone groove is weak (Pl. 5 fig. 1) ; this is also the case in *A. lemanense* and *A. incisivum.* The antecrochet is strong, extending across the medisinus and joining the base of the metaloph in M.29252 and probably also in M.29250. A crista is not present, but a swelling at the base of the medisinus in M.29252 suggests the presence of a crochet. The medisinus is narrow and a wide tubercle crosses the lingual opening. A strong cingulum is present in *A. lemanense* but in *A. incisivum* the condition is similar to the Zelten form, with a strong antero-posterior tubercle in the opening of the medisinus. The labial face of the P^4 is very high in M.29267 and shallowly concave as in *A. incisivum,* but in contrast to *A. lemanense* in which the face is slightly convex owing to the weakness of the paracone rib. This rib is very strong in M.29252 and in M.29267 but is not preserved in M.29250. A labial cingulum is not present in M.29252, M.29250, M.29267, *A. incisivum* or *A. lemanense,* but the anterior and posterior cingula are strong.

The lingual and labial regions of the right P^3 and the lingual region of the left P^3 are preserved on M.29252, and the almost complete left and right third premolars are preserved on M.29250. Unfortunately the latter specimens are heavily worn and the crowns are broken and obscured by matrix. The labial and lingual regions of the P^3 are also preserved (M.29267) from the uncollected skull ; these parts cannot be joined but almost the complete tooth is preserved. The protocone constriction is nearly lost as in *A. incisivum.* The antecrochet extends across the medisinus as in the P^4 and the molars, but it is weaker than in *A. lemanense* or *A. incisivum.* A crochet was probably present as indicated by a swelling of the anterior face of the metaloph on M.29267 and the left P^3 of M.29252. The labial face of the tooth is shallowly convex with a weak central swelling, and the paracone rib is much weaker than in the P^4 ; this is also true of *A. lemanense* but may be partly a wear factor. The anterior and posterior cingula are strong, and there is a strong tubercle at the lingual opening of the medifossette as in the P^4.

P^2 is preserved on the left side of M.29252 and on both sides of M.29250. It has a wide ectoloph and a relatively short protoloph and metaloph as in *A. incisivum* and *A. lemanense.* Strong anterior and posterior cingula are present, and the tubercle in the medisinus extends anteriorly almost joining the anterior cingulum ; in *A. lemanense* the lingual cingulum is very strong, but in *A. incisivum* it is weaker and similar to that of M.29252.

The dentitions of *Aceratherium* from Gebel Zelten agree with those of *A. lemanense* and *A. incisivum,* but are distinct from both. From published descriptions and figures of *A. acutirostratum* (Deraniyagala 1951a, 1953 ; Hooijer 1963, 1966), the

TABLE 3

The upper dentition of *Aceratherium campbelli*

	M.29252		M.29266	M.29250		M.29255	M.29267	*A. acutirostratum*		*A. incisivum*	*D. leakyi*
	r.	*l.*		*r.*	*l.*			Congo	E. Africa		
I¹											
Antero-posterior length	46	46	37	–	–	–	–	–	–	48	38
Transverse width	18	19	15	–	–	–	–	–	–	17	18
Total length	70	71	57	–	–	–	–	–	–	95	–
P¹											
Antero-posterior length	23	24	–	22	24	–	–	–	–	25	–
Maximum transverse width	20	21	–	20	21	–	–	–	–	20	–
P²											
Antero-posterior length	30	31	–	29	*c* 28	–	–	32	–	32	26
Anterior transverse width	30	–	–	*c* 34	–	–	–	–	–	40	34
Posterior transverse width	37	–	–	*c* 37	–	–	–	–	–	44	36
P³											
Antero-posterior length	–	42	–	35	35	–	*c* 36	–	32	35	29
Anterior transverse width	–	–	–	49	48	–	–	–	46	54	43
Posterior transverse width	–	48	–	–	49	–	–	–	42	53	44

P⁴											
Antero-posterior length	–	47	–	45	–	–	45	46	–	37	31
Anterior transverse width	–	62	–	c 60	–	–	–	60	–	59	51
Posterior transverse width	–	56	–	55	–	–	–	53	46	55	49
M¹											
Antero-posterior length	–	51	–	c 47	–	–	–	–	52	42	36
Anterior transverse width	–	68	–	c 64	–	–	–	–	62	54	50
Posterior transverse width	–	–	–	–	–	–	–	–	56	48	46
M²											
Antero-posterior length	–	–	–	c 50	–	–	–	–	56	43	41
Anterior transverse width	–	–	–	–	–	–	–	–	64	58	55
Posterior transverse width	–	–	–	–	–	–	–	–	57	59	46
M³			M.29254								
Antero-posterior length	–	–	47	–	–	c 47	–	–	57	45	42
Anterior transverse width	–	–	49	–	–	49	–	–	62	51	51
Length of outer face	–	–	55	–	–	54	–	–	65	59	52
Length of molar row	–	–	–	–	c 150	–	–	–	c 154	130	–
Total length of tooth row	–	–	–	–	270	–	–	–	–	260	–

agreement is closer than with the European species, which supports similarities of the skull.

Lower dentition. Lower incisors are not known, but their presence is indicated by the mandibles (M.29259 & B.U.22025). If the identification of these specimens with *Aceratherium* is correct, then this animal had short rooted incisors, the root ending anterior to the P_1.

Lower dentition: *cheek teeth.* Mandible B.U.22025 contains the alveoli of the cheek teeth; two isolated cheek teeth M.29254 and M.29257 are also identified with *Aceratherium.* The latter is lightly worn and is probably a P_4, while the former is unerupted and is probably an M_3. A mandibular fragment (M.29259) – with P_2 and P_3 erupted, a partially erupted P_4, an almost complete and erupted M_1 and fragments of M_2 – is also identified with *Aceratherium.* These specimens all agree closely with the cheek teeth of *Aceratherium incisivum* (M.375); they carry strong labial grooves and are relatively wide.

The lightly worn P_3 (Pl. 7 figs. 1, 2) is almost fully molariform, with well-developed metalophid and hypolophid; the labial groove is strong (Pl. 7 fig. 2) and extends to the base of the crown. The anterior lingual valley is shallower than the posterior and swells lingually well above the base of the crown; as a result the anterior valley is lost after medium wear, a feature in which the tooth resembles *D. sumatrensis.* The tooth also resembles *A. incisivum* and *D. leakyi* (M.18921).

The P_4 is not fully erupted in M.29259 but M.29257 (Pl. 4 fig. 5) agrees closely with this tooth and is probably also a P_4. The tooth is fully molariform and relatively wide; the anterior valley is again shallower than the posterior and would be lost first in wear. The labial groove is very deep in both specimens.

Each molar carries a deep labial groove (Pl. 7 fig. 2 & Pl. 4 fig. 4) and a lingual cingulum is present in the anterior region of M.29254 (Pl. 4 fig. 4). The molars are low crowned and may be distinguished from those of *Brachypotherium* on this basis as well as the strength of the labial groove.

Cranial and dental features of A. campbelli: a summary.

The upper dentition of the Zelten form is characteristically acerathere in main features. The presence of a strong protocone constriction, especially on the two more anterior molars, the narrow lingual entrance of the medisinus, the strength of the antecrochet and the flatness of the ectoloph serve to distinguish this dentition from that of *D. leakyi*, and at the same time to ally it with *A. acutirostratum.*

The cranial features are difficult to interpret. The eye is low on the skull and anteriorly situated; the facial region is long and the nasal notch more anterior than in *A. acutirostratum*, though more posterior than in *D. leakyi* (Hooijer 1966 pl. 1). A frontal eminence and presumably a frontal horn were not present, but a small nasal horn was probably present as indicated by the weak nasal eminence and rugosity of the bone surface in this region. Frontal and very strong nasal eminences are present in *D. leakyi* but neither are present in *A. acutirostratum.* The temporal crests, occipital crests, nasals, supraoccipital region and basicranial regions differ widely in *A. campbelli* and *A. acutirostratum.*

TABLE 4

Lower dentition of *Aceratherium campbelli*

	M.29259	M.29257	M.29258	*A. acutirostratum*	*A. incisivum*	*D. leakyi*	*A. lemanense*
P_1							
Antero-posterior length	4 root	–	–	–	–	18	–
Width	5 only	–	–	–	–	11	–
P_2							
Antero-posterior length	27	–	–	–	26	26	–
Anterior transverse width	14	–	–	–	19	16	–
Posterior transverse width	17	–	–	–	23	17	–
P_3							
Antero-posterior length	32	–	–	36	35	31	–
Anterior transverse width	22	–	–	20	24	21	–
Posterior transverse width	26	–	–	22	29	23	–
P_4							
Antero-posterior length	*c* 32	35	–	–	37	35	35
Anterior transverse width	*c* 23	26	–	25	31	26	26
Posterior transverse width	*c* 28	28	–	26	31	28	28
M_1							
Antero-posterior length	40	–	–	–	43	–	42
Anterior transverse width	30	–	–	26	35	29	36
Posterior transverse width	31	–	–	29	36	30	35
M_2							
Antero-posterior length	–	–	–	48	45	41	52
Anterior transverse width	–	–	–	30	35	32	35
Posterior transverse width	–	–	–	31	35	31	35
M_3							
Antero-posterior length	–	–	46	53	43	44	53
Anterior transverse width	–	–	28	30	32	30	35
Posterior transverse width	–	–	27	29	30	28	34

The only other early Miocene rhinoceros from Africa with which this species could be confused is *Chilotheridium*, which occurs in the Bukwa fauna (Hooijer 1971, and probably those identified as *Chilotherium*, Walker 1968, 1969). However, the chances of confusion here are very slight as *Chilotheridium* has higher cheek teeth in which the antecrochet is very strong and curves basally towards the entrance of the medisinus, a feature which does not occur in *A. campbelli*.

Post-cranial. The post-cranial material identified with the long-limbed rhinoceroses is more abundant than that identified with *Brachypotherium*. It all appears to belong to the same genus which is probably *Aceratherium*.

Post-Cranial Material.

M.29284 : proximal fragment of a right Mc.III.
B.U.22031 : proximal fragment of a right Mt.III.
B.U.22032 : distal end of a Mt.III.
M.29287 : right astragalus.
B.U.22034 : right astragalus.
M.29289 : left astragalus.
B.U.22036 : left astragalus.
B.U.22037 : almost complete, right Mt.IV.
B.U.22038 : proximal region of a right Mt.II.
B.U.22039 : proximal region of a left Mt.III.
B.U.22040 : almost complete, right Mt.IV.
B.U.22041 : almost complete, right Mc.IV.
B.U.22042 : complete, right Mc.II.
B.U.22043 : phalange I of a posterior median digit.
B.U.22044 : lateral hind first phalange.
B.U.22045 : lateral hind first phalange.
B.U.22046 : lateral hind first phalange.
B.U.22047 : lateral hind first phalange.
B.U.22048 : phalange II of a median digit.
B.U.22049 : lateral hind first phalange.

Description.

Metacarpals. A right Mc.II (B.U.22042) is complete but the distal end is slightly eroded. The bone is long, slender (Table 5) and almost straight (Pl. 5 fig. 2). Its distal end is narrow with a weak posterior keel. The bone surface is smooth anteriorly, but the posterior face exhibits some roughening of the surface, partly sculpturing and partly due to erosion. The proximal end of the bone is very flattened transversely and is triangular ; the medial and lateral faces are slightly concave proximally. The proximal facet is convex antero-posteriorly and transversely ; a lateral facet is not visible but may have been eroded away. On the Mc.II of the East African long-limbed rhinoceroses (M.18842 : Hooijer 1966 pl. 12 fig. 4) the lateral face carries an antero-posteriorly elongate facet which faces laterally, and articulates partly with the medial facet of the Mc.III and partly with the mediodistal facet of the magnum. In *R. unicornis* (M.O.1961.5.10.1) the lateral facet of the Mc.II is sharply divided into a large facet facing medio-proximally and a small anterior facet facing disto-medially; the latter articulates with a small facet on the Mc.III. The lateral facets are similar to this in *D. sumatrensis* (M.O.1949.1.11.1), but the anterior facet is much larger. This anterior facet is absent in the Mc.II from Gebel Zelten (M.29300), and the corresponding facet in the Mc.III is also absent.

A proximal fragment of the right Mc.III (M.29284) is much narrower than the Mc.III of the short-limbed form (M.29275) and the medial proximal facet is narrower and more deeply concave. The bone is swollen in the proximo-medial corner of the anterior face but the swelling is far smaller than the large tuberosity which is developed in the Mc.III of the short-limbed form. The Gebel Zelten Mc.III fragment agrees closely with an Mc.III from East Africa (M.18841 : Hooijer 1966 pl. 12 figs. 2, 3), and with that of *D. schleiermacheri* (M.1281) from Eppelsheim. The medial facet is similar in size, shape and concavity and the lateral facet is also similar.

A right Mc.IV (B.U.22041) is badly eroded proximally and shattered distally, with a fragment missing from the lateral face half-way along the shaft, and with only the lateral distal region preserved. The bone is strongly curved laterally (Pl. 5 fig. 5), as in the fourth metacarpals from East Africa (M.18814 : Hooijer 1966 pl. 12 fig. 3 & M.18811 : Hooijer 1966 pl. 12 fig. 1). However, the Gebel Zelten specimen is more slender (Table 5) than the East African specimens. The proximal facet is triangular and transversely concave; it is much narrower than that of M.18814 from East Africa, and its medial facets are smaller in agreement with the lateral facets of the Mc.III, which are also small.

There can be little doubt that these metacarpals belong to the same species; they indicate a long-limbed, highly cursorial animal in which the Mc.III was dominant and the side-toes were reduced further than in the East African long-limbed rhinoceroses. It is unfortunate that a complete Mc.III is not known, but its length can be estimated from the lengths of the Mc.II and the Mc.IV and must have approached that of *D. schleirmacheri*, lying in the region 180–200 mm.

Astragalus. Four almost complete astragali – M.29287, M.29289, B.U.22036 and B.U.22034 – and several fragments are identified with the long-limbed rhinoceroses and agree closely in anatomy with the astragalus of *D. sumatrensis* (M.O. 1949.1.11.1), with astragali from Europe of *A. incisivum* (M.1290 : Kaup 1834 pl. 15 fig. 2) and with those from East Africa (listed Hooijer 1966 : Table 42). The astragali from Gebel Zelten show variation in size and anatomical details such as size of facets, but in all cases the median height is similar to the width, and the ratio of the median height to total width is higher than in the short-limbed form (Tables 6 and 13).

Metatarsals. The proximal ends of left and right second metatarsals (B.U.22039 & B.U.22038) are preserved; the latter is more complete with about three-quarters of the shaft preserved. The bone is strongly curved medially as in *R. unicornis* and *D. sumatrensis*; it is long and slender with transversely convex anterior and concave posterior faces. The lateral face is plane where it rests against Mt.III. The proximal facet is transversely concave and antero-posteriorly convex; it is subtriangular in shape. An elongate, single lateral facet is present on B.U.22038, but on B.U.22039 paired anterior and posterior facets are present; these articulate with the Mt.III and the disto-medial facets of the cuneiform. In *R. unicornis*

TABLE 5

Aceratherium : Metacarpals

	Mc.II		Mc.III		Mc.IV	
	B.U.22042	E. Africa M.18843	M.29284	E. Africa M.18837	B.U.22041	E. Africa M.18814
Length	142	–	–	–	142	150
Proximal width	23	43	62	49	37	51
Proximal antero-posterior depth	36	47	47	38	35	47
Middle width	22	38	–	43	24	35
Middle antero-posterior depth	21	–	–	18	17	22
Distal width	28	–	–	–	–	50
Distal antero-posterior depth	24	–	–	–	30	41
Width of distal trochlea	28	–	–	–	–	44

TABLE 6

Aceratherium : Astragalus

				E. African forms		*D. schleiermacheri*	*A. incisivum*	*D. sumatrensis*
	M.29289	M.29287	B.U.22034	M.18881	M.18875	M.2786	M.2755	
Lateral height	61	*c* 65	*c* 73	67	66	79	79	67
Median height	60	67	71	65	68	74	67	66
Total width	57	77	–	82	73	94	86	69
Ratio median height/total width	1·05	0·87	–	0·79	0·93	0·78	0·78	0·97
Trochlea width	59	63	–	65	64	79	78	67
Width of distal facets	64	64	–	73	68	76	68	66

Table 7

Aceratherium : Metatarsals

	Mt.II			Mt.III			Mt.IV		
	B.U.22039	B.U.22038	E. Africa	B.U.22031	B.U.22032	E. Africa	B.U.22037	B.U.22040	E. Africa
Length	–	–	162	–	–	180	151	165	160
Proximal width	30	29	29	55	–	57	47	41	44
Proximal antero-posterior depth	48	49	48	42	–	49	44	38	46
Middle width	29	34	32	51	–	50	27	28	29
Middle antero-posterior depth	29	20	30	25	–	25	25	23	–
Distal width	–	–	42	–	64	60	36	34	38
Distal antero-posterior depth	–	–	41	–	43	41	34	33	40
Width of distal trochlea	–	–	36	–	54	51	30	31	37

(M.O.1961.5.10.1) paired facets are present in this position on the Mt.II, and in *D. sumatrensis* a very large single facet is present.

The proximal region of the right Mt.III (B.U.22031) is preserved, and a distal region (B.U.22032) which is tentatively identified as a Mt.III. The shaft is compressed antero-posteriorly with concave posterior and convex anterior faces. The proximal facet is shallowly concave rising laterally. The bone is transversely narrower than that figured by Fourtau (1920 p. 46 fig. 30) from *B. snowi* and its lateral projection is less pronounced. Paired lateral facets are present for articulation with Mt.IV; these are similar to those of *R. unicornis.* The distal region (B.U.22032) carries a deep transverse channel on the anterior face immediately proximal to the condyle. The facet is relatively small on the anterior face and carries a weak keel on the distal and posterior regions. B.U.22031 and B.U.22032 have no parts in common, and the minimum length of the Mt.III is estimated as 200 mm which agrees closely with that estimated for the Mc.III and is in the right range to accommodate the Mt.IV which is completely known.

Two specimens of the right fourth metatarsal are known (B.U.22037 & B.U.22040). The former is virtually complete lacking only a small part of the posterior distal region, and the latter lacks the proximal and distal posterior regions. The bone is curved laterally (Pl. 5 fig. 6), but less so than the Mt.II; its shaft is long and slender (Pl. 5 fig. 6) and the distal facet is narrow. The proximal facet is very large, swelling sharply from the shaft; it is shallowly convex whereas in *D. sumatrensis* and *R. unicornis* it is shallowly concave. The median facets for articulation with the Mt.III are poorly marked due to erosion of the surface, but they appear to agree with those of *R. unicornis.*

Phalanges. A phalange I of a posterior median digit (B.U.22043) is of the long-limbed type and is longer and wider than those from East Africa. A phalange II of a median digit (B.U.22048) may be anterior or posterior, but is also of the long-limbed type.

Four lateral, hind, first phalanges are preserved; they are similar in size and proportions to those of the long-limbed rhinoceroses from East Africa.

Genus ***BRACHYPOTHERIUM*** Roger 1904

DIAGNOSIS. Large hornless rhinoceroses: I^1 and I_2 developed as tusks; upper molars with strong antecrochet; crista and crochet usually well developed; protocone strongly constricted; limbs short.

COMMENTS. This group of large, heavy-bodied rhinoceroses is basically defined by the presence of upper tusks (I^1) and short limbs and feet. Although the genus was established in 1904, confusion between *Teleoceras* and *Brachypotherium* persisted for the next twenty years, and the name *Teleoceras* was given to the North African brachypothere by Fourtau (1918, 1920). Stehlin (1925), with particular reference to *B. brachypus*, expressed his preference for the use of the name *Brachypotherium* rather than *Teleoceras* as the generic identity had never been demonstrated. After this the generic distinction between the Old and New World forms was usually maintained. The main, easily usable, distinction between the two genera lies in the metapodials, which are more abbreviated in *Teleoceras* than in *Brachypotherium* (Hooijer 1968 and pers. comm.).

Brachypotherium snowi (Fourtau) 1918

DIAGNOSIS. A large species of *Brachypotherium* from the Upper Oligocene or Lower Miocene of North Africa. Upper cheek teeth measuring about 300 mm P^1–M^3. Feet less shortened than in the advanced brachypotheres. Outer faces of lower cheek teeth flattened.

COMMENTS. This species was established under the generic name *Teleoceras* by Fourtau but, as explained above, it was later regarded as a member of the genus *Brachypotherium*. The date of Fourtau's original description seems to be confused ; he gives the date 1918, but Hopwood and Hollyfield (1954) state that this paper ' is a ghost ' and cite all Fourtau's species as being established in 1920 – the date of the publication housed in the British Museum (Natural History). Simons (1969) states that a copy of the 1918 publication is housed in the Osborn Library, American Museum of Natural History. I have treated the 1918 date for the description of the Moghara species as valid.

AGE AND LOCALITY. Lower Miocene ; Moghara, and Siwa, Egypt ; and Gebel Zelten, Libya.

MATERIAL.

M.29382 : a cast of the holotype ; a right maxilla with P^2 to M^3 all heavily worn (figured Fourtau 1920 p. 38 fig. 26).
M.29384 : a cast of the P^3 exhibiting heavy wear (figured Fourtau 1920 p. 39 fig. 2a).
M.29269 : a fragment of right maxilla with M^1 and M^2 exhibiting medium wear.
M.29268 : a left maxillary fragment with P^2 and P^3 exhibiting wear.
M.29260 : a fragment of a right mandible with P_3–M_1.
M.29261 : a fragment of a right mandible with an unerupted M_3.
M.29262 : a fragment of a right mandible with D_2–D_4 in wear and M_1 almost fully erupted.
M.29263 : an I_2 lacking the tip of the crown and most of the root.
M.29264 : a mandibular symphysis with the I_1 and I_2 alveoli preserved.
M.29265 : an isolated I_1.
M.25126 : the horizontal ramus of a right mandible.
B.U.22025 : a left mandible with D_1 to D_4 and an unerupted M_1.
B.U.22026 : a left vertical ramus of a mandible.

DESCRIPTION.

Mandible. M.25126 is an almost complete horizontal ramus which is shallower than that of *R. unicornis* and agrees in depth with M.29260. In M.25126 the cheek teeth are represented by the roots only with the exception of M_3, on which a fragment of enamel is preserved ; a two rooted P_1 was present on this specimen. The length of the tooth row agrees with that of *B. snowi* from Moghara. The symphysis begins at the level of the middle of P_2 and on M.25126 the anterior mental foramen also lies at this level; this foramen is slightly more anteriorly situated in M.29260. The roots of the I_2 extend below the P_2 in M.25126, M.29260 and M.29264. M.29265 is a complete symphysial region, with both I_2 alveloi preserved and the roots of the first incisors (Pl 6 fig. 3). The I_2 alveoli run almost parallel to each other, and the teeth would have pointed anteriorly and slightly upwards.

A complete ascending ramus (B.U.22026) is preserved and identified with *Brachypotherium*, mainly on a size basis. The leading edge of the ramus is very broad with a shallow concavity in the region postero-dorsal to M_3; this is also present on M.29261 and B.U.22025. M.29261 is larger than would be expected in *Aceratherium*. The medial face of the ramus is concave in the lower part, with a large mandibular foramen which is directed postero-dorsally; the lateral face is plane and the angle is only slightly pronounced. The coronoid process is long antero-posteriorly and low as in *D. schleiermacheri*, and in contrast to *A. incisivum* in which it is short and high. The coronoid of *B. aurelianensis* is similar to that of *B. snowi* in shape and orientation. The condyle is wide and a strong post-condylar process is present as in *B. aurelianensis*, *D. schleiermacheri* and *A. incisivum*. The mandibular fragment found in association with the uncollected skull (Pl. 3) has a length of about 220 mm from the lowest point of the angle to the top of the condyle as measured from the photograph. In B.U.22026 this distance is 280 mm.

Upper dentition. The species *B. snowi* was established on the basis of an upper right tooth row in which all the teeth were heavily worn, a more lightly worn, isolated P^3, and a very lightly worn P^4. Casts of the upper tooth row (M.29382) and the isolated P^3 (M.29384) were available for comparisons. Other specimens used are: M.33527 – an upper, left tooth series of *B. brachypus* from Villefranche d'Astrac (Gers), which is made up of teeth from different individuals and was also used by Hooijer (1966 p. 145) in his description of *B. heinzelini*; M.7622 – an isolated left M^2 of *B. aurelianensis* from Chilleurs-aux-bois (Loiret), France; M.40743 – an isolated M^1 or M^2 of *B. goldfussi* from Sansan, Gers, France.

The specimens of *B. snowi* from Gebel Zelten consist of a maxillary fragment with M^1 and M^2 (M.29269: Pl. 6 fig. 2), and another fragment with P^2 and P^3 (M.29268: Pl. 6 fig. 1). The molars are badly cracked, but M^2 is complete and M^1 lacks only the antero-lingual and lingual regions; these teeth are only lightly worn, but the premolars are very heavily worn.

M^2 has a strong protocone constriction with anterior and posterior grooves, and a shallow hypocone groove is also present. Constriction and grooves of similar strength are present in *B. brachypus* and *B. goldfussi*, but they are stronger in *B. aurelianensis*. The strength of these features is to some extent related to the strength of the antecrochet; this is strong in M.29269 and in *B. snowi* from Moghara; it is similar in strength in *B. brachypus* and *B. goldfussi*, but is stronger in *B. aurelianensis*. A weak fold of the enamel near the labial end of the medisinus suggests the presence of a crista, and a strong crochet is present; a crochet of similar strength is present in *B. brachypus* but in *B. goldfussi* and *B. aurelianensis* the crochet is stronger. A crista is not present in specimens of *B. brachypus* figured by Deperet (1887 pl. 23 figs. 1 & 1a) and Mayet (1909 p. 25 fig. 11), nor in *B. aurelianensis* figured in Mayet (1908 pl. 2 fig. 5); this suggests that the crista is variable in the brachypotheres. The metaloph is flexed posteriorly in M.29269 (Pl. 6 fig. 2) as in *B. brachypus* and *B. aurelianensis* ; this flexion is stronger than in the Gebel Zelten acerathere and produces a deep postfossette. The parastyle and paracone ribs are very strong and similar to those of *B. snowi* from Moghara, with a weaker labial extension than in *B. brachypus*, *B. aurelianensis* or *B. goldfussi*. The labial face of the ectoloph is concave with a swelling opposite the mesostyle. The anterior and posterior cingula are strong as in M.29382 from Moghara. A small swelling of enamel at the base of the postero-labial corner may represent a labial cingulum, but otherwise labial and lingual cingula are absent except at the entrance to the medisinus ; this contrasts with *B. brachypus* and *B. goldfussi* in which strong lingual and labial cingula are present. However, variation in the strength or presence of the cingula occurs (Viret 1961).

An isolated M^3 from Siwa, Libyan Desert, Egypt, was identified with *B. snowi* (Hamilton 1973). It is smaller than the M^3 of the type dentition (Fourtau 1920 p. 38 fig. 26), and lacks the antero-lingual rib which is produced from the face of the hypocone ; it also differs in several features from the M^3 of *B. heinzelini* (M.10632).

The P^3 (M.29268) agrees closely with that described by Fourtau (1920 p. 39 fig. 3a) ; it is very heavily worn (Pl. 6 fig. 1) and details of the crown are largely worn away. The P^2 (M.29268) is also similar to that of *B. snowi* from Moghara (M.29382).

The upper dentition of *B. snowi* compares closely in general features with that of *B. brachypus*, but the parastyle and paracone region is less pronounced antero-lingually, and the lingual cingula are either weak or totally absent. There are also differences in the strengths of the antecrochet, crochet and crista, but these features exhibit variation in *B. brachypus*, and their significance here cannot be assessed as so few specimens of *B. snowi* are known.

B. heinzelini from East Africa and the Congo is represented in the British Museum (Natural History) collections by an isolated M^3 (M.10632), which was figured as an unidentified rhinocerotid by Andrews (1914 pp. 176–177 pl. 28 fig. 3), and was identified with *B. heinzelini* by Hooijer (1966 pl. 7 fig. 3). Good dental material of this species appears to be relatively scarce, as Hooijer (1963, 1966) figures very little material. The holotype is a P^4 from Sinda, Congo, which was briefly compared with *B. snowi* by Hooijer (1963 p. 46). The tooth appears to be very similar in the two species, but a labial cingulum is present in *B. heinzelini* from the Congo, though absent in the Rusinga specimen (Hooijer 1966 p. 143) and in the P^4 of *B. snowi*. The P^4 is generally longer and narrower in *B. heinzelini* than in *B. snowi*. The M^1 of *B. heinzelini* from Karungu (Hooijer 1966 pl. 6 figs. 5 & 6) is very heavily worn and appears very different in shape in comparison with that of *B. snowi*. This specimen has a labial cingulum which contrasts with the molars of *B. snowi* in which the labial cingulum is very reduced if present. An M^2 of *B. heinzelini* is also figured by Hooijer (1963 pl. 8 figs. 4–6) under the name *Aceratherium cf. tetradactylum* ; reasons for the reidentification of this specimen are given by Hooijer (1966 p. 143). This M^2 compares in general features with the Zelten specimen (Pl. 6 fig. 2), but the labial wall is more flattened, the antecrochet is stronger and the crochet appears double in the Congo specimen. The tooth also differs in size from that of *B. snowi*.

On the basis of these comparisons I think that the upper dentition of *B. snowi* is distinct from that of *B. heinzelini*.

The incidence of *Indricotherium* (*Paraceratherium*) at Sahabi, Libya, was noted by Savage (1967) and Hooijer (1968), the record being based upon an isolated rhinocerotid M^2 described as *Teleoceras aff. medicornutum* by Erasmo (1954), and identified with *Indricotherium* by Hooijer (1968) on account of its great size. This tooth is very similar to the M^2 of *B. snowi*, having a strong protocone constriction with a marked posterior protocone groove. A strong antecrochet and crista and a weak swelling suggests that a small crochet may have been present. The tooth is, however, much larger than the M^2 of *B. snowi*, having an anterior width of 99 mm, a posterior width of 92 mm and a length of 78 mm. The Sahabi fossils are of late Miocene age, and during the interval between the time of deposition of the Gebel Zelten and Sahabi an increase in size of a *Brachypotherium* stock could well have occurred. In my opinion the Sahabi specimen represents a survival of *Brachypotherium* into the late Miocene of Libya.

Lower dentition: *incisors*. A single left I_2 is preserved (M.29263 : Pl. 6 fig. 8) ; this agrees closely with the I_2 of *B. brachypus* figured by Roman & Viret (1934 pl. 11 fig. 5), and with that of *B. aurelianensis* figured by Mayet (1908 pl. 3 fig. 2), and is almost exactly the same size as these incisors. The root is elliptical in cross-section with the long diameter horizontal. This contrasts with *D. leakyi* in which the root of the incisor has a subtriangular cross-section (Hooijer 1966). The root of M.29263 is straight antero-posteriorly and curves slightly dorsally as in *B. aurelianensis* (Mayet 1908 pl. 2 fig. 2a), and in agreement with the curvature of the alveoli in M.25126 and M.29264, which also have similar cross-sections. The crown of the tooth is heavily worn but it flares laterally immediately above the root as in *B. brachypus*, *B. aurelianensis* and *Chilotheridium* (Hooijer 1971 pl. 6 figs. 1–4) ; this sort of expansion is not visible in *D. leakyi* (Hooijer 1966 pl. 4 figs. 4 & 5), *D. schleiermacheri* (M.21490), *A. incisivum* (M.253) or *A. acutirostratum* (Hooijer 1966 pl. 4 figs. 2 & 3). The tip of the crown is broken off (Pl. 6 fig. 8), but it was lance shaped with the point on the medial side. Preserved parts of the tooth agree closely with the I_2 of *B. brachypus* in which the root length is 110 mm suggesting a similar root length for M.29263 ; this agrees with the length of the alveoli in M.29264. The crown of the tooth is heavily worn with facets in two planes (Pl. 6 fig. 8). The medial facet is the more horizontal and its surface is smooth : it blends laterally into a more laterally directed facet, which has deep transverse striations indicating heavy wear against a hard object – presumably the I^1.

An isolated I_1 (M.29265 : Pl. 5 fig. 3) is preserved with fragments of the alveoli ; the tooth is tentatively identified with *B. snowi* as its root has the same cross-sectional shape as the I_1 roots in the symphysis (M.29264), though the isolated tooth is larger. The root curves dorsally and the I_1 would have projected anteriorly at approximately the same angle as the I_2. The crown is bulbous and exhibits heavy wear on its tip ; similar first lower incisors are present in *R. unicornis*.

Cheek dentition. The lower cheek teeth identified with *Brachypotherium* are larger and higher than those of *Aceratherium*. In agreement with Hooijer (1966) the depth of the groove between the hypolophid and metalophid was taken as a

TABLE 8

Upper dentition of *Brachypotherium snowi*

	B. snowi, Gebel Zelten		*B. snowi*, Moghara		*B. snowi*, Siwa	*B. heinzelini*		*B. brachypus*
	M.29269	M.29268	M.29382	M.29384	M.11966	Congo	E. Africa	M.M.33527
P^2								
Antero-posterior length	–	32	29	–	–	–	–	30
Anterior transverse width	–	39	42	–	–	–	–	39
Posterior transverse width	–	42	45	–	–	–	–	43
P^3								
Antero-posterior length	–	41	40	40	–	–	36	34
Anterior transverse width	–	60	61	60	–	–	54	51
Posterior transverse width	–	54	56	56	–	–	54	52
P^4								
Antero-posterior length	–	–	44	–	–	49	48	39
Anterior transverse width	–	–	70	–	–	62	66	58
Posterior transverse width	–	–	61	–	–	58	62	55
M^1								
Antero-posterior length	56	–	*c* 53	–	–	–	–	54
Anterior transverse width	–	–	71	–	–	–	62	70
Posterior transverse width	–	–	62	–	–	–	52	60
M^2								
Antero-posterior length	62	–	61	–	–	63	–	52
Anterior transverse width	79	–	75	–	–	77	–	68
Posterior transverse width	67	–	63	–	–	63	–	58
M^3								
Antero-posterior length	–	–	61	–	54	–	55	56
Anterior transverse width	–	–	–	–	–	–	65	68
Length of outer face	–	–	–	–	–	–	68	73

criterion on which the lower cheek teeth of *Aceratherium/Dicerorhinus* and *Brachypotherium* could be distinguished; those teeth with shallow grooves were placed with *Brachypotherium* and those with deep grooves were identified with *A. campbelli.* This distinction is, however, not invariable, teeth with shallow grooves usually belong with *Brachypotherium* but those with deep grooves may belong with either *Dicerorhinus/Aceratherium* or with *Brachypotherium.* This is demonstrated by the mandible identified with *B. snowi* by Fourtau (1920); cheek teeth on this mandible have deeper grooves than on the lower molars identified with *B. snowi* from Gebel Zelten, but its identification with *B. snowi* is probably valid (Hooijer pers. comm.). A cast of Fourtau's specimen (M.29383), lower cheek teeth of *B. brachypus* (M.33523), lower molars of *B. goldfussi* (M.238 : Kaup 1834 pl. 12 figs. 13 & 14) and a lower molar fragment of *B. heinzelini* (M.25186) were available for comparison.

The M_1 of *B. snowi* has weak anterior and posterior cingula and two small tubercles at the lingual opening of the posterior valley (Pl. 6 fig. 4). The hypolophid is much longer than the metalophid, a feature also exhibited by *B. brachypus* and *B. goldfussi,* and the labial groove is weaker than in these species, though similar in strength to that of *B. heinzelini* (M.25186).

M.29261, an unerupted lower molar, is probably an M_3; its labial groove is slightly stronger than in M.29260 but far weaker than in *Aceratherium.* The molar is relatively high and the hypolophid–metalophid junction is over 30 mm above the base of the crown. A weak posterior cingulum is present.

The P_4 is more elongate than in *B. brachypus* and appears less antero-posteriorly compressed, as the lingual valleys are more open and the anterior end of the metalophid is less flexed lingually (Pl. 6 fig. 4). The hypolophid also exhibits less flexion, cingula are absent and the labial groove is very shallow (Pl. 6 fig. 6). The P_4 of *B. snowi* from Moghara has a deeper labial groove than that of M.29260 and although heavily worn it appears that the crown was lower. The posterior lingual valley was deeper and its opening extends more nearly to the base of the crown. The P_3 of M.29260 differs from *B. brachypus* in the same features as the P_4, it is more elongate and less antero-posteriorly compressed, the lingual valleys are more open and the anterior end of the metalophid is less flexed lingually. A weak cingulum is present on the antero-labial corner only, whereas in *B. brachypus* cingula are present on the four corners though in M.33523 they do not join across the faces of the tooth. The groove at the junction of the metalophid and hypolophid is relatively strong on the P_3 of *B. brachypus* and on *B. snowi* from Moghara but in M.29260 it is very shallow. The P_3 of *B. snowi* from Moghara resembles the P_4 in having a heavily worn and probably initially lower crown with a deeper posterior lingual valley. A P_2 of *B. snowi* is not known from Gebel Zelten but Fourtau (1920) describes a P_2 and a fragment of the P_1 of *B. snowi* from Moghara. A P_1 was probably not present in M.29260 but the presence of a D_1 in B.U.22025 suggests that the presence of a P_1 may have been variable.

Descriptions of the deciduous lower dentitions of rhinoceroses are rare in the literature. Roman & Viret (1934 pl. 10 fig. 9) describe and figure a lower deciduous cheek tooth of *B. brachypus* which is probably a D_3 and Hooijer (1966 pl. 4 fig. 1) figures the D_2–D_4 of *Dicerorhinus leakyi* from Napak, Uganda. M.29262 is a crushed

TABLE 9

Lower dentition of *Brachypotherium snowi*

INCISOR	M.29263
Width of crown	40
Antero-posterior length of crown	26
Transverse diameter of crown	36
Antero-posterior diameter of root	–

CHEEK TEETH	M.29260	M.29261	M.29262	Moghara	*B. heinzelini* E. Africa	*B. brachypus* M.33523
P_2						
Antero-posterior length	*c* 22	–	–	28	–	–
Anterior transverse width	–	–	–	18	–	–
Posterior transverse width	–	–	–	22	–	–
P_3						
Antero-posterior length	34	–	–	36	–	39
Anterior transverse width	20	–	–	25	–	24
Posterior transverse width	24	–	–	26	–	28
P_4						
Antero-posterior length	42	–	–	–	–	49
Anterior transverse width	20	–	–	–	–	28
Posterior transverse width	28	–	–	28	–	32
M_1						
Antero-posterior length	46	–	51	–	–	46
Anterior transverse width	27	–	–	–	–	31
Posterior transverse width	30	–	–	–	29	–
M_2						
Antero-posterior length	–	–	–	57	56	54
Anterior transverse width	–	–	–	–	37	33
Posterior transverse width	–	–	–	37	35	33
M_3						
Antero-posterior length	–	53	–	*c* 62	–	61
Anterior transverse width	–	31	–		31	33
Posterior transverse width	–	*c* 30	–	*c* 34	29	33

fragment of a right mandible containing the almost complete D_2–D_4 and the labial and anterior regions of the partially erupted M_1 (Pl. 7 figs. 3 & 4). This specimen is identified with *B. snowi* as the M_1 agree with other lower molars of this species. B.U.22025 is also identified with *Brachypotherium*; it contains D_1–D_4 and an unerupted M_1 (Pl. 8). The D_1 is small, single rooted and peg-like. D_2 is triangular and trilobed with two labial and two lingual grooves. D_3 is elongate and molariform; it exhibits medium wear in B.U.22025 and heavier wear in M.29262. The anterior end of the anterior lophid is forked as in the D_3 of *B. brachypus* (Roman & Viret 1934 pl. 10 fig. 9). The D_3 lacks a labial cingulum. Hooijer (1971) discusses a D_3 from Ngorora which he identifies with *Brachypotherium.* This tooth has a weak labial cingulum and a D_3 of *Brachypotherium* from Lothagam also has a weak cingulum. Both of these teeth are in the same size range as M.29262 and B.U.22025.

The D_4 is molariform with well-developed lophids and a weakly developed labial groove; it is about the same length as the D_3 and carries a cingulum in its antero-lingual region. The fragment of the M_1 in M.29262 is hypsodont and the metalophid is shorter than the hypolophid as in M.29260; the labial groove is also shallow in M.29262. The unerupted M_1 of B.U.22025 has a slightly stronger labial groove but is larger and more hypsodont than the M_1 of the Zelten *Aceratherium.* Fourtau also described an isolated M_2 which had a flattened outer face and carried a cingulum anteriorly. This agrees with *B. brachypus* and a weak swelling on the face of the tooth in this region is also present on the M_1 of M.29260. The M_2 described by Fourtau is relatively large, having a length of 57 mm. This isolated molar agrees in size with M.29260 and M.29262 and probably belongs with the same species. Fourtau also gives the dimensions of the alveoli of the M_3 from the same mandible as the M_2; this tooth had alveoli of length 62 mm and width 34 mm (Table 9), which is larger than M.29261 but within the same size range and far outside the size range of M.29254 which is here identified with *Aceratherium.*

TABLE 10

Lower deciduous dentition of *Brachypotherium snowi*

	M.29262	B.U.22025
D_1		
Antero-posterior length	–	8
Transverse width	–	5
D_2		
Antero-posterior length	31	29
Anterior transverse width	15	13
Posterior transverse width	20	17
D_3		
Antero-posterior length	47	42
Anterior transverse width	24	18
Posterior transverse width	25	21
D_4		
Antero-posterior length	49	45
Anterior transverse width	27	21
Posterior transverse width	30	25

Post-cranial material. Dental evidence suggests that only a single short-limbed rhinoceros was present at Gebel Zelten in early Miocene times, and post-cranial elements characteristic of short-limbed rhinoceroses may therefore be assigned to the genus *Brachypotherium*. It is likely that *Brachypotherium* was the only short-limbed rhinoceros in Africa in early Miocene times, as records of *Chilotherium* from Africa south of the Sahara are no longer valid, and *Chilotheridium* is a longer-limbed form.

MATERIAL.

M.29274 : a complete right radius.
M.29275 : a complete left, third metacarpal.
B.U.22027 : a badly shattered third metacarpal.
B.U.22028 : a cracked but nearly complete, right, second metacarpal.
B.U.22029 : a complete, right, fourth metacarpal.
M.29278 : a left astragalus.
B.U.22030 : a left astragalus.
M.29279 : a left astragalus.
B.U.22031 : the proximal region of a first phalange of the right, anterior, median digit.
B.U.22032 : the second phalange of a median digit.
B.U.22033 : the second phalange of a median digit.
M.29277 : a left astragalus from Arongo Uyoma, East Africa.

DESCRIPTION.

Radius. A complete right radius (M.29274) agrees closely with that of *B. heinzelini* (M.18908) described by Hooijer (1966 pl. 9 fig. 1). The Gebel Zelten specimen is slightly more slender (Table 11), and the distal end is less massive than in *B. heinzelini*. This is the only rhinocerotid radius from Gebel Zelten ; it is shorter and thicker than those of the East African long-limbed rhinoceroses, and is smaller than the radii of *B. brachypus* and *B. stehlini*. In his 1971 paper Hooijer mentions the presence of a small facet on the radius of *Chilotheridium* which articulates with the cuneiform ; such a facet is not present on M.29274 or M.18908.

TABLE 11

Brachypotherium Post-cranial material

Radius

	M.29274	*B. heinzelini*	*Chilotheridium*
Median length	282	293	315
Proximal width	86	95	94
Middle width (maximum)	49	52	50
Distal width (maximum)	84	95	95

Metacarpals. Metacarpals of *B. heinzelini* from East Africa were available for comparison ; these included Mc.III and Mc.IV (M.18813 & M.18812 : Hooijer 1966 pl. 10 figs. 1 & 2), and Mc.IV (M.18822 : Hooijer 1966 pl. 10 fig. 8).

The Mc.II from Gebel Zelten is large and relatively thick ; the proximal medial facet is concave, rising laterally with a new facet starting at the top of this rise and sloping disto-laterally. The anterior face of the metacarpal is heavily sculptured, and the posterior face carries several tubercular swellings of the bone. This metacarpal agrees in general shape with that figured by Hooijer (1966 pl. 10 fig. 3), but the distal facet is longer on the anterior face and the medio-proximal swelling of the bone is weaker in the Gebel Zelten specimen than in that from East Africa.

The third metacarpals (M.29275 & B.U.22027) agree closely with the Mc.III of *B. heinzelini.* M.29275 (Pl. 6 figs. 5 & 9) is slightly longer than the East African specimen (Table 12), but it is also more massive with a very strong anterior tuberosity in the proximal region and proximal facets for Mc.IV which are larger and more widely separated than in *B. heinzelini.* The distal facet of M.29275 is narrower than in *B. heinzelini* and extends further proximally on the anterior face of the bone ; this facet is also deeper antero-posteriorly in the Gebel Zelten specimen.

The Mc.IV (B.U.22029) is smaller and rather more slender than the East African specimens (M.18812 & M.18813) ; its proximo-medial region is only slightly swollen whereas in the East African Mc.IV this region carries a strong swelling. B.U.22029 is slightly bent laterally but to a smaller extent than in the East African specimens and its distal facet is smaller.

These three metacarpals are difficult to interpret as the Mc.II is large relative to the Mc.III, and similarly the Mc.IV is relatively small ; this is interpreted as falling within the degree of variation of a single species as the alternative interpretation – that there were three short-limbed forms at Gebel Zelten – is unlikely. The Mc.III agrees closely with that of *B. heinzelini,* but is from a slightly larger animal which agrees with differences in the size of the dentition. This metacarpal also agrees closely in size with the Mt.III described from Moghara (Fourtau 1920 p. 46 & text fig. 30), which was identified as *B. snowi.* Metatarsals identifiable with the short-limbed rhinoceroses are not known from Gebel Zelten or East Africa, but Hooijer (1966) compared the Mc.III of *B. heinzelini* with the Mt.III of *B. snowi* by comparing both with *B. brachypus* in which, as Hooijer (1966 table 16) demonstrates, there is considerable variation in the size of the metacarpals and the metatarsals. By this somewhat roundabout method Hooijer deduced that : ' the Rusinga *B. heinzelini* is more progressive than that of Moghara in Egypt in having more shortened metapodials '. The direct comparison of the Mc.III from Gebel Zelten with that from East Africa demonstrates that the metapodials have approximately the same proportions.

Astragalus. The astragali of *Brachypotherium* are very compressed and the median height never exceeds the width, whereas in the long-limbed rhinoceroses the median height of the astragalus may be equal to or greater than the width. Astragali of *B. brachypus* (M.33529) from Villefranch d'Astrac and (M.7760) from Thenay were available for comparison ; both were also used by Hooijer (1966). Astragali of *B. heinzelini* are figured by Hooijer (1963 pl. V fig. 10 & 1966 pl. 14 fig. 3). The Zelten astragali are all from the left side. B.U.22030 and M.29278 agree in size with the African and European specimens, but M.29279 (Pl. 6 fig. 7) is larger though similar in proportions and details of the facets.

TABLE 12

Brachypotherium Post-cranial material

Metacarpals

	Mc. II			Mc. III			
	B.U.22028	*B. heinzelini*	*Chilotheridium*	M.29275	B.U.22027	*B. heinzelini*	*Chilotheridium*
Length	149	125	123	146	140	137	140
Proximal width	51	52	41	75	–	65	49
Proximal antero-posterior depth	50	47	36	61	–	52	38
Middle width	53	45	33	60	–	*c* 55	39
Middle antero-posterior depth	31	25	17	25	–	26	17
Distal width	57	50	43	74	–	74	52
Distal antero-posterior depth	51	38	37	55	–	47	39
Width of distal trochlea	48	40	37	58	–	58	45

	Mc. IV		
	B.U.22029	*B. heinzelini*	*Chilotheridium*
Length	103	110	115
Proximal width	31	44	37
Proximal antero-posterior depth	35	53	44
Middle width	31	37	26
Middle antero-posterior depth	20	25	18
Distal width	41	53	41
Distal antero-posterior depth	–	38	33
Width of distal trochlea	32	45	36

TABLE 13

Brachypotherium Post-cranial material

Astragalus

	Gebel Zelten			*B. brachypus*		Arongo Uyoma	*B. heinzelini*
	M.29278	B.U.22030	M.29279	M.33529	M.7760	M.29277	Congo[1]
Lateral height	69	68	73	58	60	58	68
Medial height	67	68	75	64	63	55	–
Total width	105	93	113	100	99	87	102
Ratio medial height/total width							
Trochlea width	75	75	90	85	80	75	–
Width of distal facets	91	84	95	85	86	68	–

([1] after Hooijer 1963)

An isolated astragalus from Arongo Uyoma, East Africa (M.29277), was missed by Hooijer (1966). Its details are given here, as the astragali of short-limbed rhinoceroses are relatively rare from East Africa and this is the only such astragalus in the British Museum (Natural History) collection. The bone is from the left side, and the lateral half is complete except on the antero-lateral face of the left trochlear ridge from which a chip of bone is missing. The medial distal part is well preserved but the medial proximal region is broken off. This astragalus is similar in size and general features to the Gebel Zelten specimens (M.29278 & B.U.22030), and also agrees with the astragali of *B. heinzelini*. The disto-lateral facet is correspondingly smaller ; this is, however, only a slight variation, and I think this specimen is probably from *B. heinzelini*.

Phalanges. The proximal region of the first phalange of the right, anterior, median digit (B.U.22031) carries a strong swelling of the bone which forms a collar around the bone just distal to the articulation. A similar swelling is present on the phalange I of *B. heinzelini* (Hooijer 1966 pl. 10 fig. 6), which suggests that this bone may belong with the short-limbed rhinoceroses. The posterior face of the bone falls away anteriorly indicating that it was much compressed. The proximal facet of the phalange is narrower than that of *B. heinzelini* and also narrower than the distal facet of Mc.III (M.29275) identified with *B. snowi*.

Two second phalanges of median digits – B.U.22032 and B.U.22033 – are more proximo-distally compressed than in the long-limbed rhinoceroses and probably belong with the short-limbed group. However, each is longer than the phalange II of *B. heinzelini* (M.18862 : Hooijer 1966 pl. 10 fig. 7).

A few carpals and tarsals are probably identifiable with *B. snowi*, but these are described with the other elements from Gebel Zelten as identification is less certain and direct comparison is simplified.

Rhinocerotidae indet.

The following specimens cannot be definitely assigned to either groups of rhinoceroses known from Gebel Zelten.

M.29305 : an isolated right scaphoid.
B.U.22051 : fragment of a lunar.
B.U.22050 : fragment of a lunar.
M.29306 : cuneiform.
M.29307 : cuneiform.
B.U.22052 : cuneiform.
B.U.22053 : left trapezoid.
M.29293 : calcaneum.
B.U.22054 : right calcaneum.
B.U.22055 : right calcaneum.
B.U.22056 : right calcaneum.
B.U.22057 : left calcaneum.
B.U.22058 : right calcaneum.
M.10364 : calcaneum from East Africa.

M.29308 : right cuboid.
B.U.22059 : left cuboid.
B.U.22060 : right cuboid.
B.U.22062 : left navicular.
M.29310 : right navicular.
B.U.22061 : right navicular.
B.U.22064, B.U.22063, B.U.22065, B.U.22066, M.29312 : ectocuneiforms.

Scaphoid. An isolated right scaphoid M.29305 is large and agrees closely in size with M.18897 from East Africa (Hooijer 1966 table 30 & pl. 14 fig. 6), and with that of *D. schleiermacheri* (M.1218 : Kaup 1834 pl. 13 fig. 9). The distal articular facet of the radius and corresponding facet of the scaphoid agree, suggesting that the scaphoid belongs with the short limbed rhinoceroses, but this may be a size factor.

TABLE 14

Rhinocerotidae indet. Post-cranial material

Scaphoid

	M.29305	E. Africa M.18897
Posterior height	68	71
Anterior height	60	54
Proximal width	49	49
Distal width	34	33
Antero-posterior middle length	68	66

Lunar. Two fragmentary lunars are known. B.U.22051 lacks the proximal radius facet and the posterior region of the bone is broken off. B.U.22050 consists of the anterior region only ; the anterior proximal facet for articulation with the radius is preserved and the distal unciform facet. The radius facet is antero-posteriorly convex and similar to that of M.18907 from East Africa (Hooijer 1966 p. 163) ; this facet is transversely narrower than in *R. unicornis* (M.O.1961.6.10.1). B.U.22051 is deeper proximo-distally than in *R. unicornis*, agreeing with M.18907 from East Africa. The distal facets for the magnum and unciform are less concave than in M.18907 ; the unciform facet agrees closely with that of *R. unicornis* but the magnum facet is smaller and shallower.

TABLE 15

Rhinocerotidae indet. Post-cranial material

Lunar

			E. Africa	
	B.U.22051	B.U.22050	M.18906	M.18907
Anterior height	–	55	45	48
Proximal width	–	44	45	–
Greatest antero-posterior length	*c* 68	–	–	67

Cuneiform. The three cuneiforms are all complete and all are larger than those from East Africa (Table 16). M.29306 is more compressed proximo-distally than the other two, and is very wide transversely and long antero-posteriorly. The proximal facet for the ulna is antero-posteriorly concave and transversely convex giving a saddle-shaped form ; this facet remains wide laterally whereas in M.29307 and B.U.22052 it tapers to a point laterally ; this also occurs in *R. unicornis* and *D. schleiermacheri* and the three specimens from East Africa (M.18903, M.25184 & M.18904). The facet for the pisiform is large and triangular. The distal facet for articulation with the unciform is more shallowly concave than in M.29307 or B.U.22052. M.29306 carries a large tubercle disto-laterally ; this swelling is far larger than any of the East African specimens, *R. unicornis, D. sumatrensis*, M.29307 or B.U.22052. Features of M.29306 suggest very strongly that it belongs with the short-limbed rhinoceroses, and it agrees closely with a cuneiform from Gers, France (M.33537), which probably belongs to *B. brachypus*.

M.29307 and B.U.22052 are long proximo-distally, the former less so than the latter (Table 16). In features of the facets these specimens agree closely with the cuneiform of *R. unicornis* and contrast with M.29306 as described above. These two specimens probably belong with the long-limbed rhinoceroses.

Trapezoid. An isolated left trapezoid is longer proximo-distally than that of *R. unicornis* and as a result its proximal and distal facets do not meet. The bone is broken antero-laterally.

Calcaneum. The nomenclature applied here to the calcaneum is after Schaeffer (1947). Calcanea from Gebel Zelten exhibit variation in size and features of the facets. The tuber calcis varies in length and the shaft is very thick in M.29293 and B.U.22054 but is transversely flattened in the other four specimens. The astragalocalcaneal facet is strongly convex proximo-distally in M.29293 and B.U.22054 as in *D. schleiermacheri* (M.2785 : Kaup 1834 pl. 13 fig. 10) and *A. incisivum* (M.1288 : pl. 15 fig. 11), but in the other four specimens this facet rises steeply from its distal region and curves very sharply. It then flattens out and continues for some distance along the proximal face of the tuber, thus giving two regions – a vertical and a horizontal – of approximately equal size, at right angles to each other.

The sustentaculum is strong and wide in M.29293, with a wide, almost circular sustentacular facet which is shallowly concave. This region is also preserved in B.U.22025, in which it is less pronounced and carries a narrow, proximo-distally elongate, sustentacular facet. A fragment of this region is preserved on B.U.22056 and indicates a similarly shaped facet.

The astragalar facet is similar in all the specimens. The cuboid facet is antero-posteriorly concave and almost circular in M.29293 and B.U.22054, but in the other four specimens it is narrow and deeply concave transversely. The peroneal tubercle is variable in strength, being very strong in M.29293 and B.U.22054, slightly weaker in B.U.22055 and B.U.22056 and very weak in B.U.22057 and B.U.22058. A second tubercle on the lateral face lying behind and slightly proximal to the peroneal tubercle is very strong in M.29293 and B.U.22054, but is weak in the other four specimens.

TABLE 16

Rhinocerotidae indet. Post-cranial material

Cuneiform

					E. Africa		*B. brachypus* ?
	M.29306	M.29307	B.U.22052	M.25184	M.18903	M.18994	M.33637
Anterior height	60	58	63	50	38	–	48
Distal width	73	55	51	36	32	33	50
Proximal antero-posterior length	44	38	37	27	26	32	40
Greatest horizontal diameter	74	58	56	40	–	42	50

TABLE 17

Rhinocerotidae indet. Post-cranial material

Trapezoid

	B.U.22053	*Chilotheridium*[1]
Anterior height	*c* 35	30
Anterior width	26	24
Greatest antero-posterior diameter	45	41
Posterior height	37	28
Posterior width	31	16

[1] After Hooijer 1971.

From the above comparison it is clear that the calcanea may be divided into two groups, one including M.29293 and B.U.22054 and the other containing the four specimens B.U.22055 to B.U.22058. The calcanea in the first group agree closely with that of *D. schleiermacheri*, and possibly belong with the long-limbed rhinoceroses.

An isolated calcaneum from East Africa (M.10364) was missed by Hooijer (1966) in his review of the East African material. As rhinocerotid calcanea are so rare in the East African collections a brief description of this specimen is given here. The shaft of the tuber calcis is transversely thickened and the distal end of the tuber is wide and heavily sculptured. The astragalocalcaneal facet is convex and similar to that of M.29293, but this region of the bone rises well above the face of the tuber calcis in M.10364, whereas in the Zelten specimens and *D. schleiermacheri* it is much lower. The sustentaculum is missing and the astragalar facet is reduced. The cuboid facet is antero-posteriorly concave and almost circular, agreeing with that of M.29293. This specimen agrees closely in general form and features with that of *D. schleiermacheri*, and in size with that of *D. leakyi* (Hooijer 1966 table 44). It may therefore be placed with the East African long-limbed rhinoceroses.

Cuboid. M.29308 is almost complete, its proximal facet is antero-posteriorly concave and transversely convex. The lateral region of the facet, for articulation with the calcaneum, is larger than the medial region of the facet and is separated from this region by a shallow antero-posterior channel. The distal facet for articulation with the Mt.IV is antero-posteriorly elongate and convex in M.29308, but in B.U.22059 it is transversely wide and convex agreeing with the facet of M.18890 from East Africa. The posterior projection of the bone is very strong in M.29308, B.U.22059, and in M.18892 from East Africa. The medial facets for articulation with the navicular and ectocuneiform are very small in M.29308 as in *R. unicornis* (M.O.1961.5.10.1), in which they are smaller than in M.18892 from East Africa. These facets are broken off B.U.22060. M.29308 is long proximo-distally and is transversely narrower than B.U.22059, B.U.22060, M.18892 or M.18890, but the antero-posterior length is similar in B.U.22059 and M.29308 (Table 19). B.U.22060 is a fragment of a high cuboid which agrees in size and proportions of its facets with B.U.22059. According to Roger (1900 p. 24), the anterior face of the cuboid is much wider than high in *Brachypotherium* : in *Aceratherium* and *Dicerorhinus* the anterior height of the cuboid is equal to or greater than the anterior width. This

TABLE 18

Rhinocerotidae indet. Post-cranial material

Calcaneum

	Gebel Zelten						E. Africa	
	M.29293	B.U.22054	B.U.22055	B.U.22056	B.U.22057	B.U.22058	M.10364	*D. leakyi*
Greatest length	131	140	119	143	143	149	136	148
Greatest width	82	–	64	–	–	–	–	89
Antero-posterior cuboid facet	36	40	40	47	45	49	46	48
Transverse cuboid facet	29	–	22	25	26	23	34	25
Greatest diameter of tuber	55	58	67	69	64	74	69	73
Transverse diameter of tuber	55	49	41	52	50	50	59	54

feature was used by Hooijer (1966 p. 176) to identify all the East African cuboids with the long-limbed rhinoceros group, and on this basis the Gebel Zelten cuboids would also be identified with the long-limbed rhinoceroses.

TABLE 19

Rhinocerotidae indet. Post-cranial material

Cuboid

	B.U.22059	B.U.22060	M.29308	M.18892	M.18890
Anterior height	49	43	43	47	45
Anterior width	44	43	39	44	36
Greatest antero-posterior width	79	79	–	73	63

Navicular. The three specimens are similar in size but exhibit several contrasting features. B.U.22062 agrees in size with M.25187 from East Africa. The astragalar facet is reduced in the antero-medial corner, giving a facet shaped almost as a right-angled triangle with the right angle postero-laterally. The bone is proximo-distally compressed and has strong antero-medial and postero-lateral tubercles. M.29310 is large and less compressed than B.U.22062. The antero-medial corner is stronger and the astragalar facet is more nearly rectangular. The bone agrees closely with M.18887 from East Africa, which was grouped with the long-limbed rhinoceroses by Hooijer (1966 p. 176). M.29311 is compressed and the bone is produced into two large tubercles in the postero-lateral and postero-medial corners. The distal facet is larger than that of M.29310, and the cuboid and posterior facets are more pronounced in B.U.22061. The strength of the tubercles agrees with features of the metapodials in the short-limbed rhinoceroses, which also carry very strong tubercles, and this suggests that B.U.22061 may belong with the short-limbed rhinoceroses. Reasons for regarding M.29310 as belonging with the long-limbed rhinoceroses are its agreement with the navicular from East Africa (M.18887), and features of the ectocuneiform mentioned below.

Ectocuneiform. The ectocuneiforms vary in size, all are deep proximo-distally as in *D. sumatrensis* but in all, as in the East African specimens (Hooijer 1966 p. 177), the postero-medial region is produced much further posteriorly than in *D. sumatrensis* or *R. unicornis.* The distal facet for the Mt.III agrees in M.29312 and B.U.22063 with the proximal facet of B.U.22031, suggesting that these specimens belong with the long-limbed rhinoceroses. The proximal facet of M.29312 also agrees closely with the distal facet of navicular M.29310 with which it can be articulated, which suggests the grouping of the three bones Mt.III (B.U.22031), navicular (M.29310) and ectocuneiform (M.29312).

CONCLUSION

The rhinoceroses of Gebel Zelten and Moghara belong to the same species, and agree at the generic level with those from the Lower Miocene of Africa south of the Sahara. *Aceratherium campbelli* is similar to *A. acutirostratum*, and derivation from a common ancestor is thought likely to have occurred probably in the late Oligocene.

TABLE 20

Rhinocerotidae indet. Post-cranial material

Navicular

	M.29310	B.U.22061	B.U.22062	M.25187	M.18887	*A. incisivum*	*R. unicornis*	*D. sumatrensis*
Greatest anterior height	29	26	23	26	31	25	30	21
Total width	52	63	51	47	53	46	58	45
Antero-posterior diameter	68	64	62	60	64	58	75	50

TABLE 21

Rhinocerotidae indet. Post-cranial material

Ectocuneiform

	Gebel Zelten					E. Africa		
	M.29312	B.U.22065	B.U.22063	B.U.22064	B.U.22066	M.18905	M.18886	*D. sumatrensis*
Anterior height	32	26	28	28	31	31	26	27
Anterior width	54	45	49	–	–	51	48	46
Antero-posterior diameter	–	50	52	52	55	51	52	40

Brachypotherium snowi is similar and probably very closely related to *B. heinzelini* and also resembles the European form *B. brachypus*. *Brachypotherium* first occurs in Europe in the early Miocene, and with reference to brachypotheres Osborn (1900) states :

> 'they have no known prototypes in the Oligocene of either Europe or America. Either the original home of this type is Africa, and if so they came into Europe with the Mastodons, or they represent an offshoot of the Aceratheriinae.' (Osborn 1900 p. 249.)

Mayet (1908) suggested that *Brachypotherium* represents a new mutation of *Aceratherium*, but Stehlin (1925) disagreed with this. The North and East African material is probably the earliest known of *Brachypotherium* but gives no indication of the ancestry of the group ; however Osborn's suggestion that Africa was the original home of the genus *Brachypotherium* is supported by the presence there of two species in the early Miocene. The European *Brachypotherium* may have entered from Africa in early Miocene times when giraffoids and proboscideans also invaded Europe.

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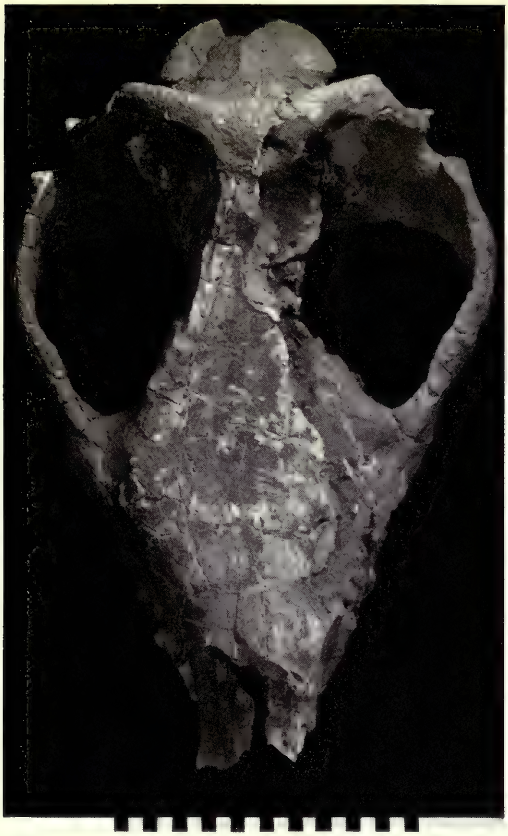
DR W. R. HAMILTON
Department of Palaeontology
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON 5W7 5BD

PLATE 1

Aceratherium campbelli sp. nov.

Fig. 1. Skull M.29250 dorsal view. (Holotype.)
Fig. 2. Skull M.29250 palatal view. (Holotype.)
Fig. 3. Skull M.29250 right lateral view. (Holotype.)



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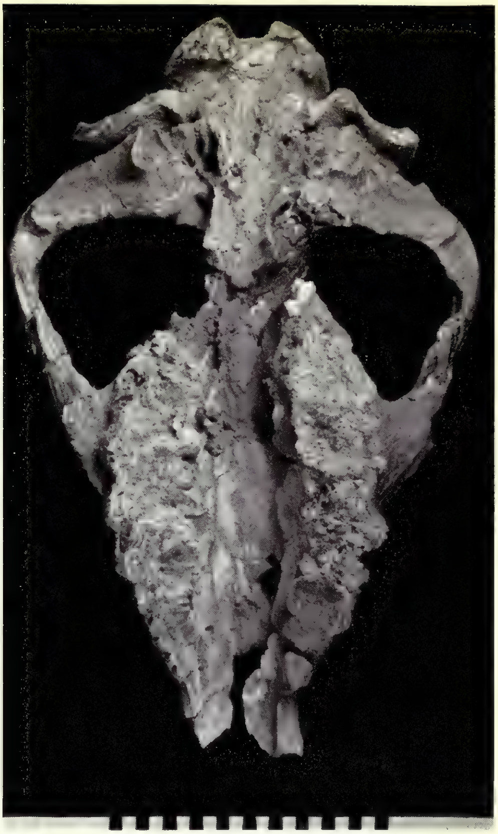

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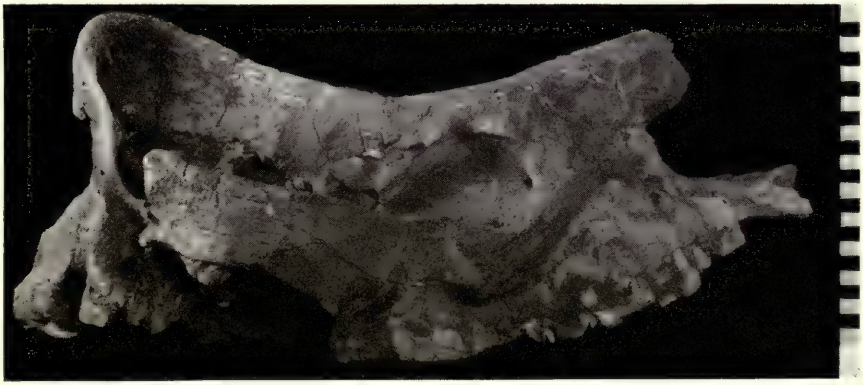

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PLATE 2

Aceratherium campbelli sp. nov.

FIG. 1. Nasals M.29251 left lateral view. × 0·6, approx.
FIG. 2. Nasals M.29251 dorsal view. × 0·6, approx.
FIG. 3. Skull M.29250 occipital region. × 0·3, approx. (Holotype.)

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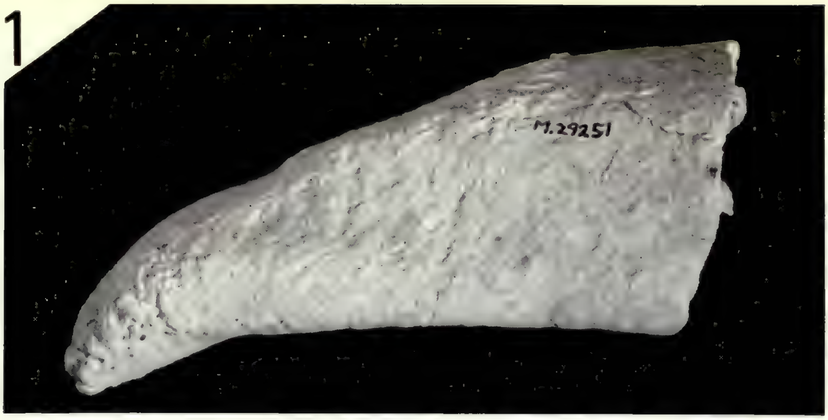

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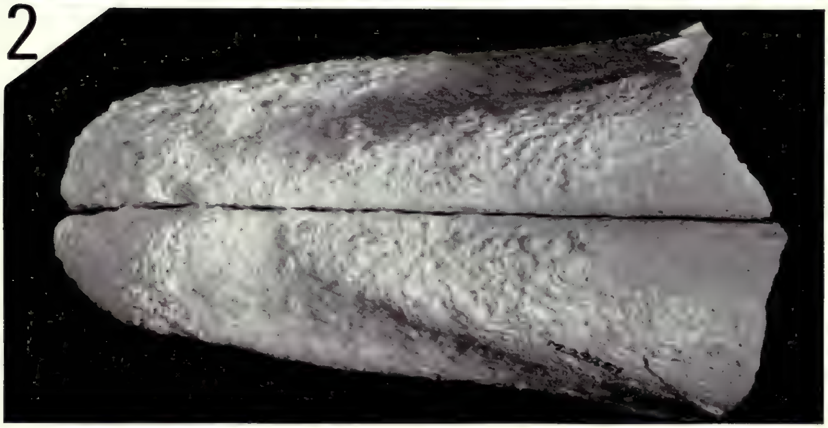

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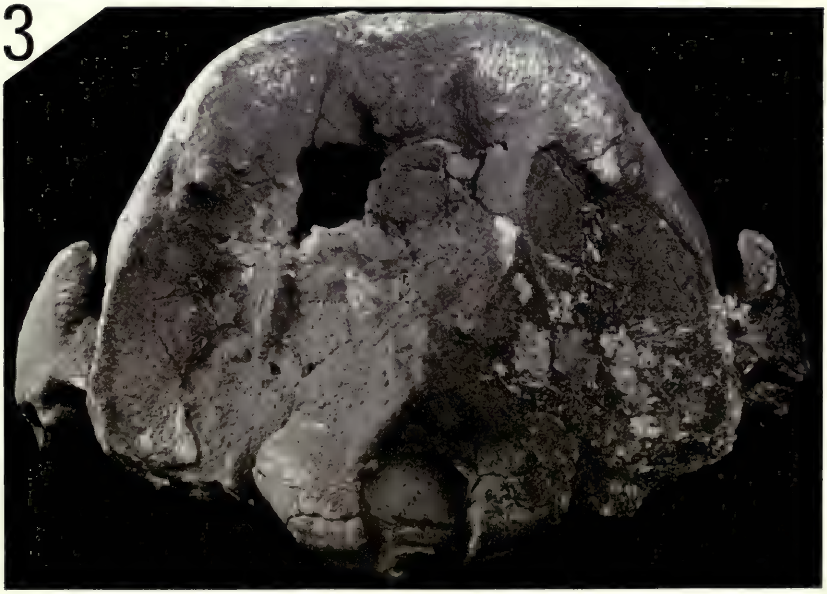


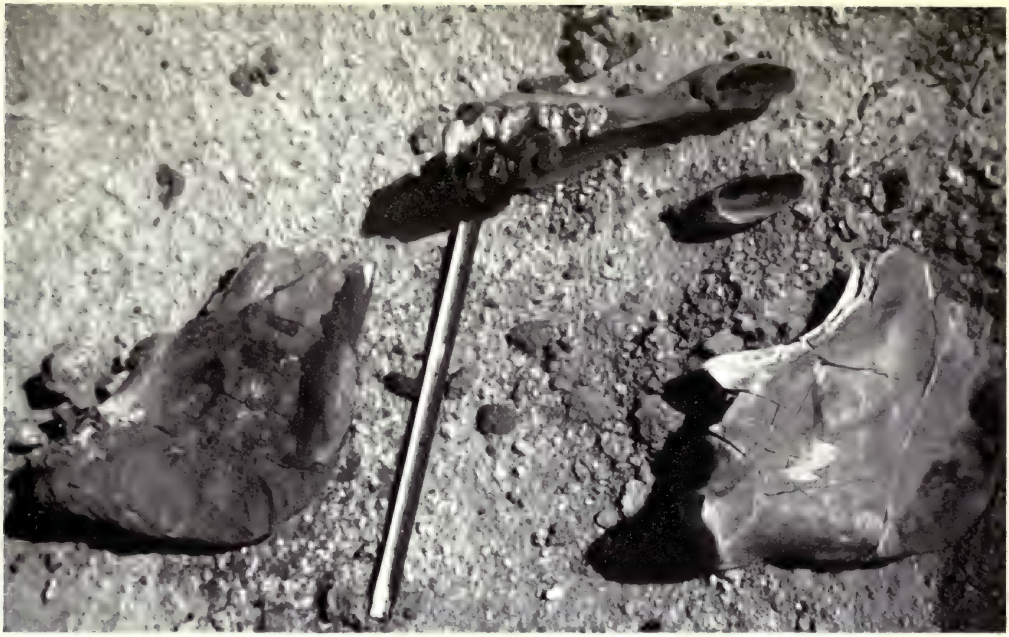
PLATE 3

Aceratherium campbelli sp. nov.

FIG. 1. Uncollected skull before excavation.

FIG. 2. Uncollected skull after excavation.

N.B. Both figures from colour transparencies which were kindly supplied by Dr R. C. Selley.



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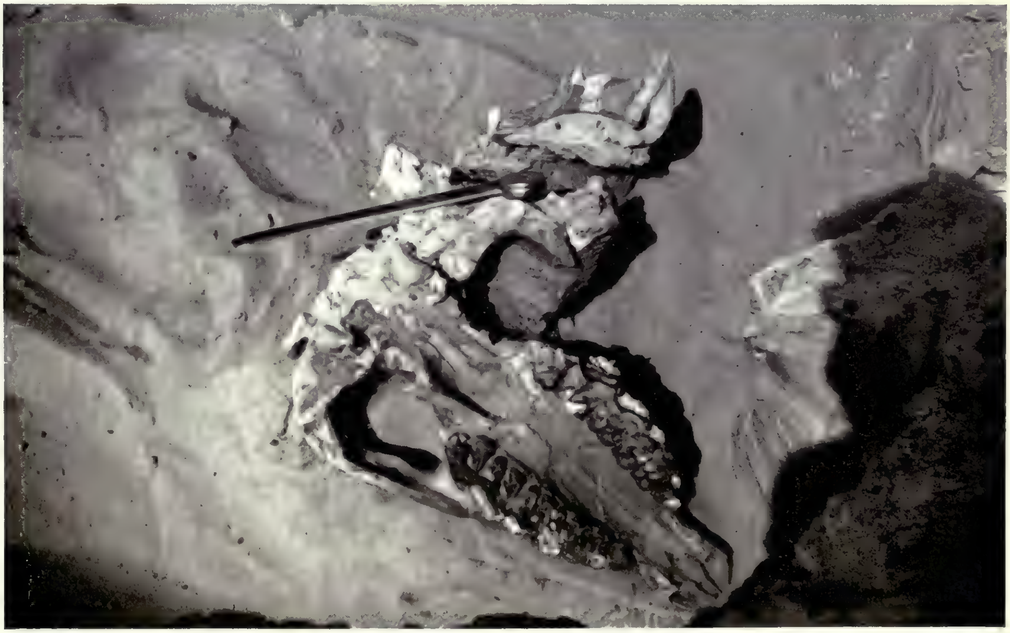

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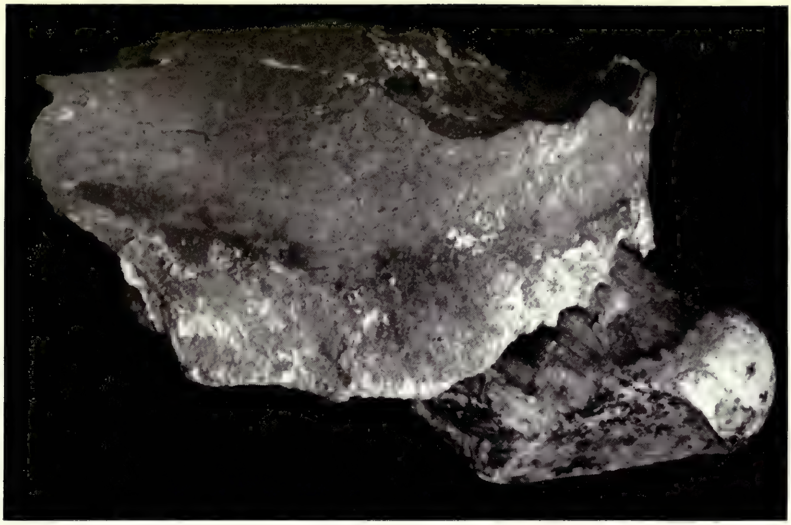
PLATE 4

Aceratherium campbelli sp. nov.

Fig. 1. Upper right incisor M.29252 lateral view. × 1, approx.
Fig. 2. M^2 lingual fragment M.29256 occlusal view. × 1, approx.
Fig. 3. M^3 M.29254 occlusal view. × 1, approx.
Fig. 4. M_3 M.29258 occlusal view. × 1, approx.
Fig. 5. P_4 M.29257 occlusal view. × 1, approx.
Fig. 6. Upper incisor which may belong with *Aceratherium* M.29266 lingual view. × 1, approx.



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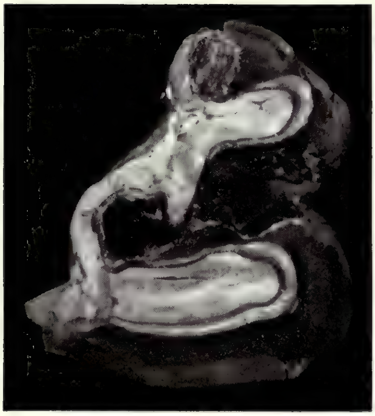

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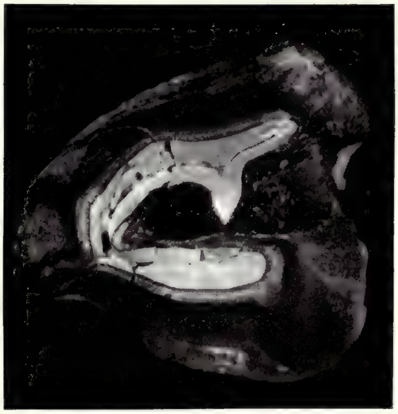

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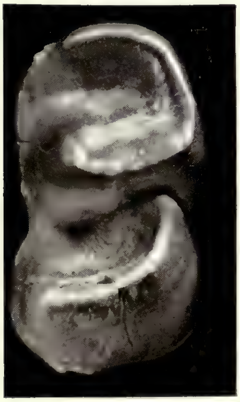

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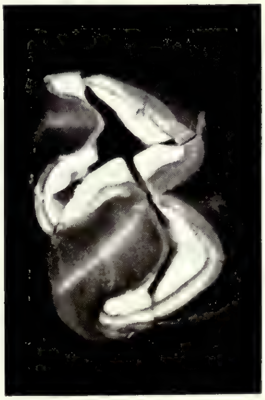

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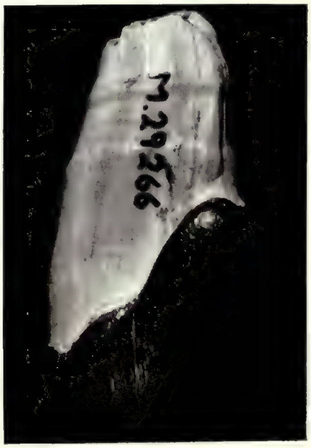

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PLATE 5

Aceratherium campbelli sp. nov.

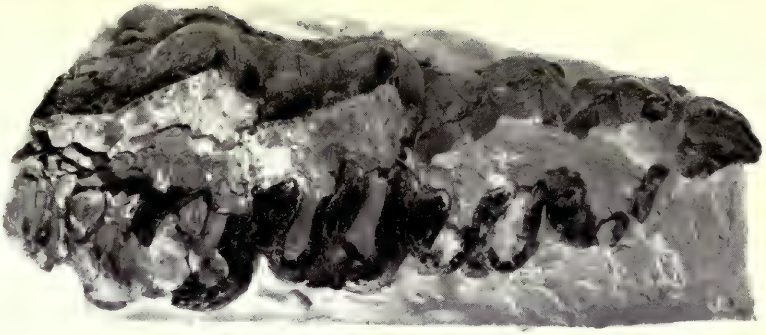
FIG. 1. Upper right cheek teeth M.29252 occlusal view. × 0·7, approx.
FIG. 2. Right second metacarpal B.U.22042 medial view. × 0·5, approx.
FIG. 5. Right fourth metacarpal B.U.22041 anterior view. × 0·6, approx.
FIG. 6. Right fourth metatarsal B.U.22037 anterior view. × 0·5, approx.

Brachypotherium snowi (Fourtau)

FIG. 3. A first incisor M.29265 anterior view. × 0·5, approx.

Rhinocerotidae indet.

FIG. 4. A left calcaneum M.29293 dorsal view. × 0·5, approx.
FIG. 7. A right calcaneum from East Africa M.10364 dorsal view. × 0·5, approx.
FIG. 8. A right calcaneum from East Africa M.10364 medial view. × 0·5, approx.



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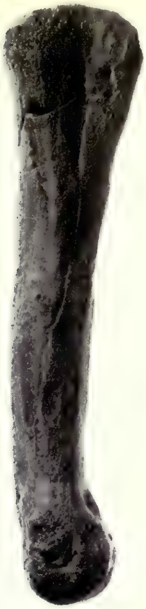

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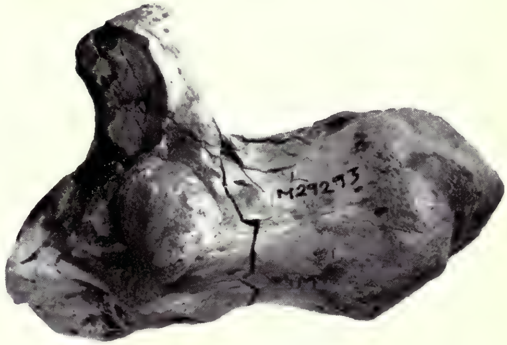

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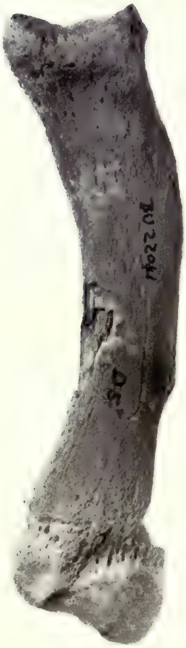

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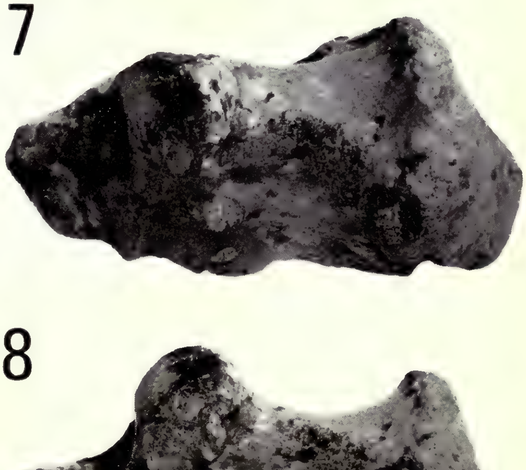

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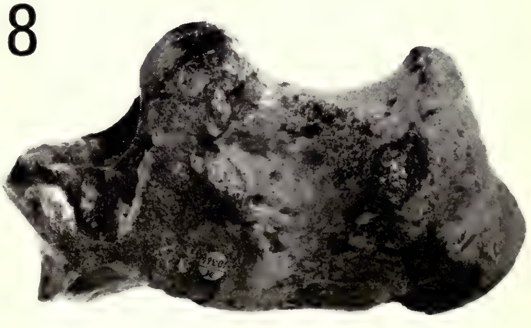
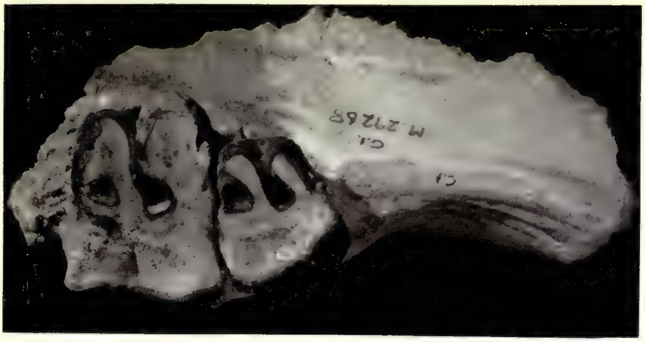


PLATE 6

Brachypotherium snowi (Fourtau)

FIG. 1.	Maxillary fragment with P^2 and P^3 M.29268 occlusal view.
FIG. 2.	M^1 and M^2 M.29269 occlusal view.
FIG. 3.	Mandibular symphysis M.29264 dorsal view.
FIG. 4.	Right mandibular fragment with P_3–M_1 M.29260 occlusal view.
FIG. 6.	Right P_3–M_1 M.29260 labial view.
FIG. 5.	Left, third metacarpal M.29275 proximal facets.
FIG. 9.	Left, third metacarpal M.29275 anterior view.
FIG. 7.	Left astragalus M.29279 anterior view.
FIG. 8.	A second, lower incisor M.29263 lingual view.

All figures × 0·5, approx.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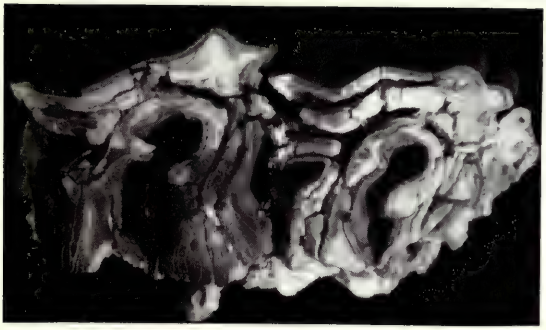

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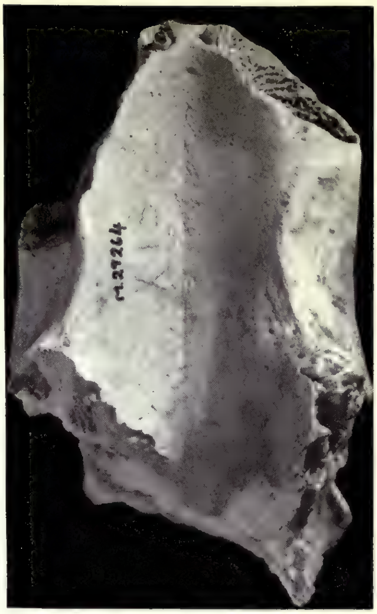

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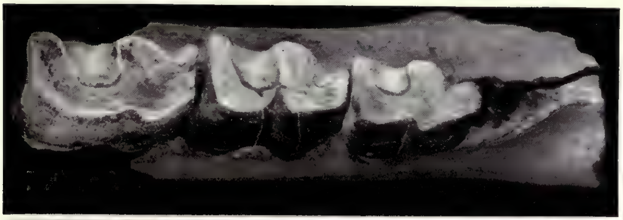

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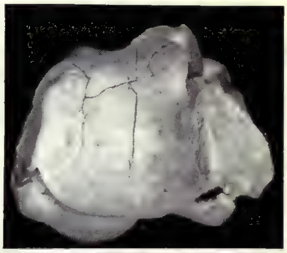

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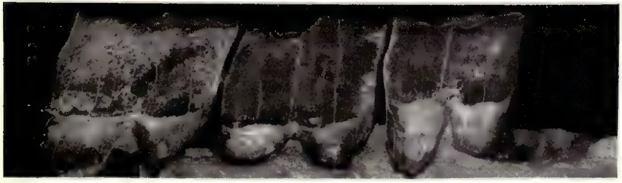

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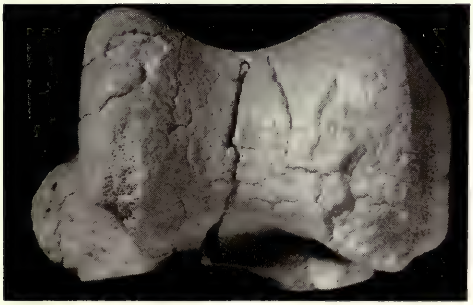

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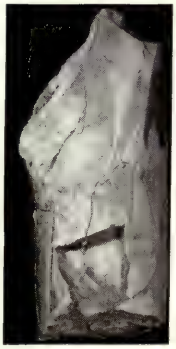

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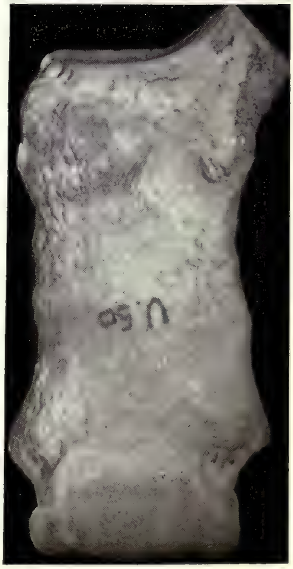

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PLATE 7

Aceratherium campbelli sp. nov.

FIG. 1. A right mandibular fragment with P_2–M_1 M.29259 occlusal view. × 0·5, approx.

FIG. 2. Right mandibular fragment M.29259 labial view. × 0·5, approx.

Brachypotherium snowi (Fourtau)

FIG. 3. A right mandibular fragment with D_2–D_4 and M_1 M.29262 occlusal view. × 0·5, approx.

FIG. 4. Right mandibular fragment with D_2–D_4 and M_1 M.29262 lateral view. × 0·5, approx.

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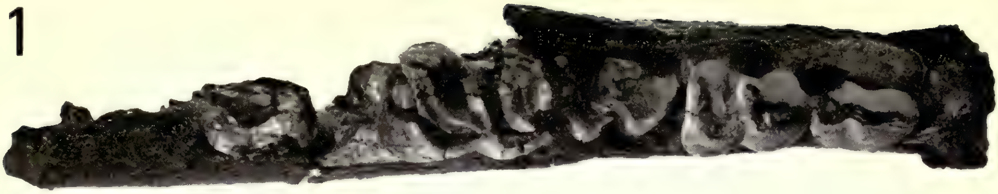

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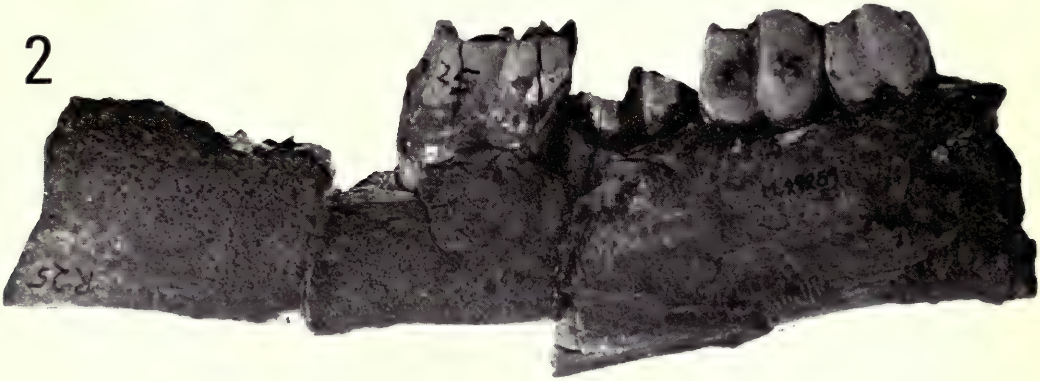

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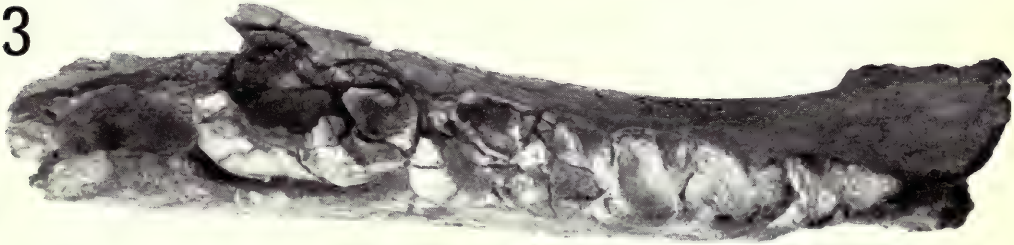

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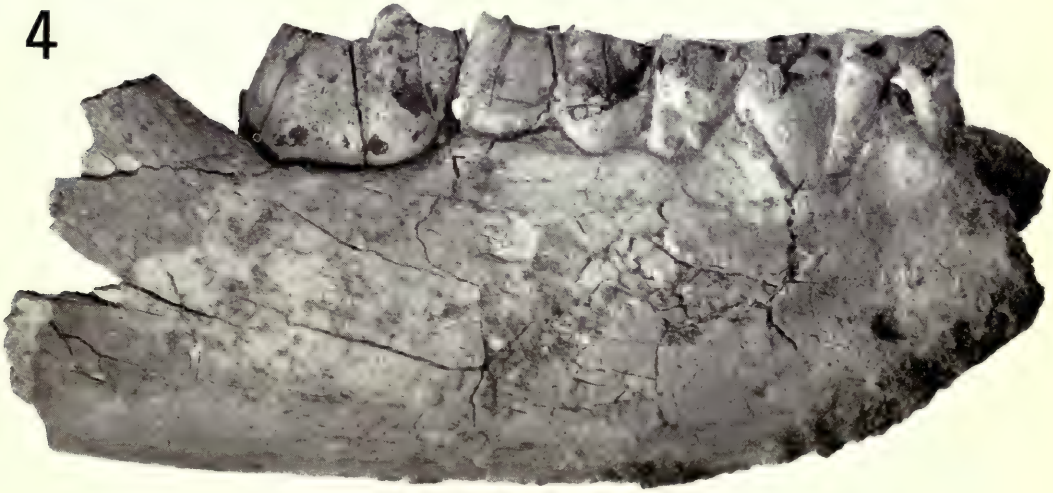
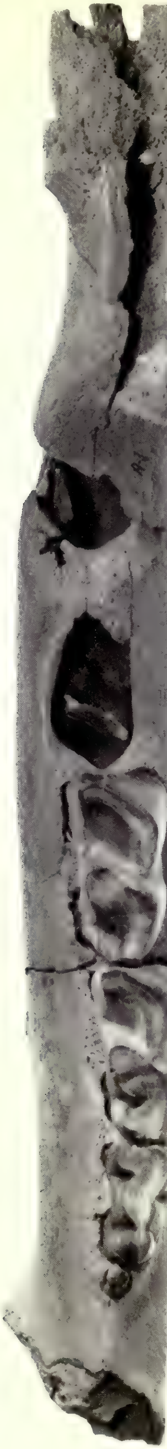


PLATE 8

Brachypotherium snowi (Fourtau)

Fig. 1. Left mandible with D_1–D_4 erupted B.U.22025 occlusal view. × 0·5, approx.

Fig. 2. Left mandible with D_1–D_4 B.U.22025 lateral view. × 0·5, approx.



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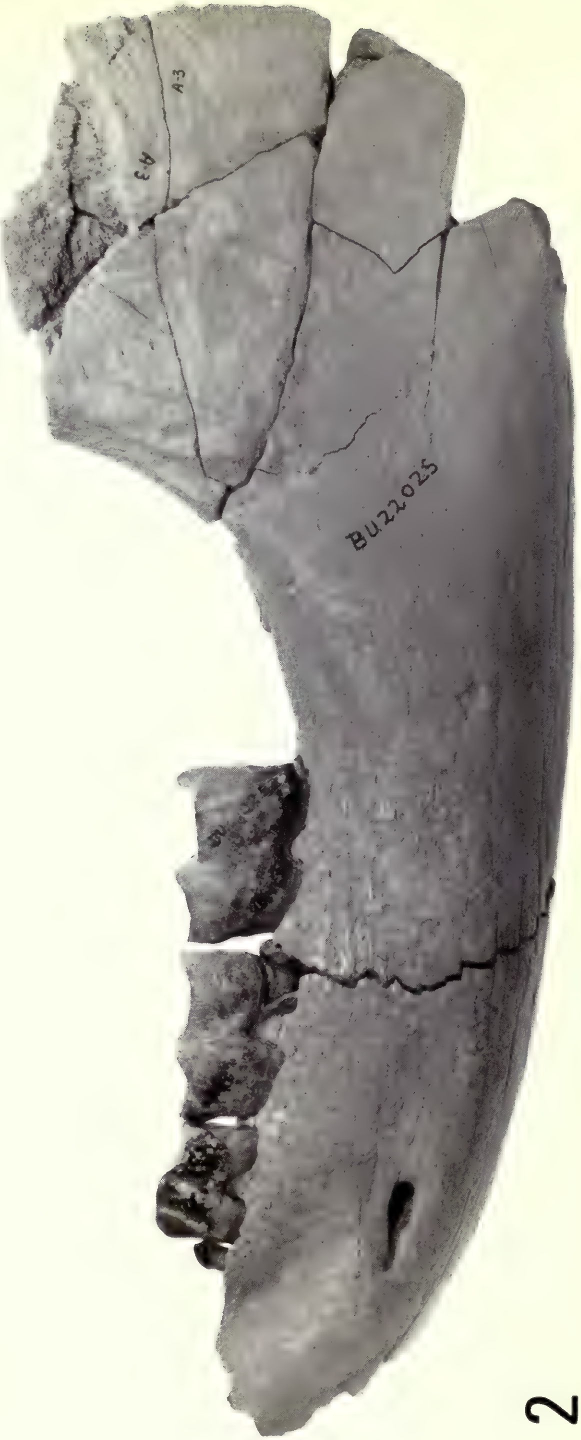
A-3
A-3
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2

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A. W. CROMPTON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
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LONDON : 1974

THE DENTITIONS AND RELATIONSHIPS OF THE SOUTHERN AFRICAN TRIASSIC MAMMALS, *ERYTHROTHERIUM PARRINGTONI* AND *MEGAZOSTRODON RUDNERAE*

BY
ALFRED WALTER CROMPTON
Department of Biology and Museum of Comparative Zoology,
Harvard University, Cambridge, Massachusetts, U.S.A.

Pp. 397–437 ; 3 *Plates*, 11 *Text-figures*

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SYNOPSIS

The dentitions of two southern African Triassic mammals, *Erythrotherium parringtoni* and *Megazostrodon rudnerae*, are described. On the basis of dentition alone, these forms seem to be closely related to the European and Chinese Triassic mammals, *Eozostrodon* (= *Morganucodon*) *parvus* and *Eozostrodon oehleri*. All of these mentioned forms are included in the Family Morganucodontidae. *Sinoconodon rigneyi*, also from the Chinese Triassic, should perhaps also be included in this family, although it has been placed in a separate family, the Sinoconodontidae. There is no justification for placing *Megazostrodon rudnerae* in this latter family.

One of the results of the reorganization and relative increase in mass and complexity of jaw musculature, which took place in the more advanced cynodonts, was that control and mobility of the lower jaw was increased. It is suggested that in the earliest and as yet undiscovered mammals, or in those cynodonts directly ancestral to mammals, this increased control permitted the longitudinal axis of the lower jaw to subscribe a triangular orbit during mastication. As a result of the transverse component of this orbit, the postcanine teeth of early mammals and their immediate ancestors were brought into closer contact than in their ancestral stock. This closer contact improved ability to break down food. Once a triangular orbit for the lower jaw was established, the characteristic features of mammalian dentitions evolved rapidly as a means of further improving efficiency. These features include single replacement of only some of the postcanine teeth, differentiation of the postcanine series into premolars and molars, consistent relationships of upper and lower molars with development of accurately matched shearing surfaces, and accurate alignment of adjoining molars.

It is shown that both the earliest known therian mammal, *Kuehneotherium*, and the early members of the non-therian mammalian stock, the Morganucodontidae, could be derived from a hypothetical ancestral group which possessed this suite of features. In the separate lines leading to therian and non-therian mammals, the ways in which the upper and lower molars contacted one another and the ways in which adjoining molars were aligned developed in slightly different patterns. These differences had far-reaching effects on the course of subsequent evolution of molar patterns and occlusion in therian and non-therian mammals.

I. INTRODUCTION

FIVE genera of Triassic mammals have been described, *Eozostrodon* (= *Morganucodon*),[1] *Kuehneotherium*, *Erythrotherium*, *Megazostrodon* and *Sinoconodon*.[2] (Selected papers dealing with these five genera are Kühne (1958), Crompton & Jenkins (1968), Hopson & Crompton (1969), Kermack, Kermack & Mussett (1968), Parrington (1971, 1973), Mills (1971), Crompton (1964), Patterson & Olson (1961) and Kermack & Kielan-Jaworowska (1971)).

The purpose of this paper is to give a detailed account and interpretation of the dentitions of *Megazostrodon rudnerae* and *Erythrotherium parringtoni*. Preliminary accounts have already been published (Crompton 1964; Crompton & Jenkins 1968; Hopson & Crompton 1969). Recently the types of both genera have been further prepared and much additional information is now available. The specimens are important because they add to the meagre body of knowledge on Triassic mammals and because both types consist of nearly complete skulls and skeletons. With full preparation it will be possible to give a skeletal reconstruction of two early mammals. This reconstruction has not previously been possible because, although the remains of *Eozostrodon parvus* are abundant, they are fragmentary. The skulls and skeletons will be described in later papers.

Detailed descriptions of the dentition of *Eozostrodon parvus* have recently been published by Parrington (1971) and Mills (1971). In a later paper Parrington (1973) has discussed differences between his and Mills' description of *Eozostrodon*. Mills (1971) has also given a detailed account of the dentition of *Eozostrodon oehleri* (= *Morganucodon oehleri*) (Rigney 1963). One of the important conclusions of Parrington's study is that *Eozostrodon parvus* had a mammalian pattern of tooth replacement with several of the milk molars being replaced by permanent premolars while the molars were never replaced. However, this form retained the reptilian feature of losing the anterior postcanines (in some cases even some of the anterior molars) either concurrent with or after the complete eruption of the postcanine dentition. Such detailed studies have tended to confirm the now generally accepted view that the Morganucodontidae ([= Eozostrodontidae], see Hopson 1970) are related to the non-therian mammalian radiation (i.e. docodonts, triconodonts,

---

[1] Unfortunately, there is no general agreement as to whether *Eozostrodon* and *Morganucodon* are synonyms. The case in favour of synonymy has been presented by Parrington (1971, 1973), and the case against by Kermack, Kermack & Mussett (1968) and Mills (1971). Whether the remains of the mammals from Wales, generally referred to as *Morganucodon watsoni*, and the type of *Eozostrodon parvus* from Somerset are included in the same taxon is perhaps not important, but it is confusing having both terms in current use. Parrington's case (1971, 1973) seems to be sound and in this paper *Eozostrodon* will be used in preference to *Morganucodon*.

[2] If the Haramiyidae prove to be mammals, the genera of this family would have to be added to the above list.

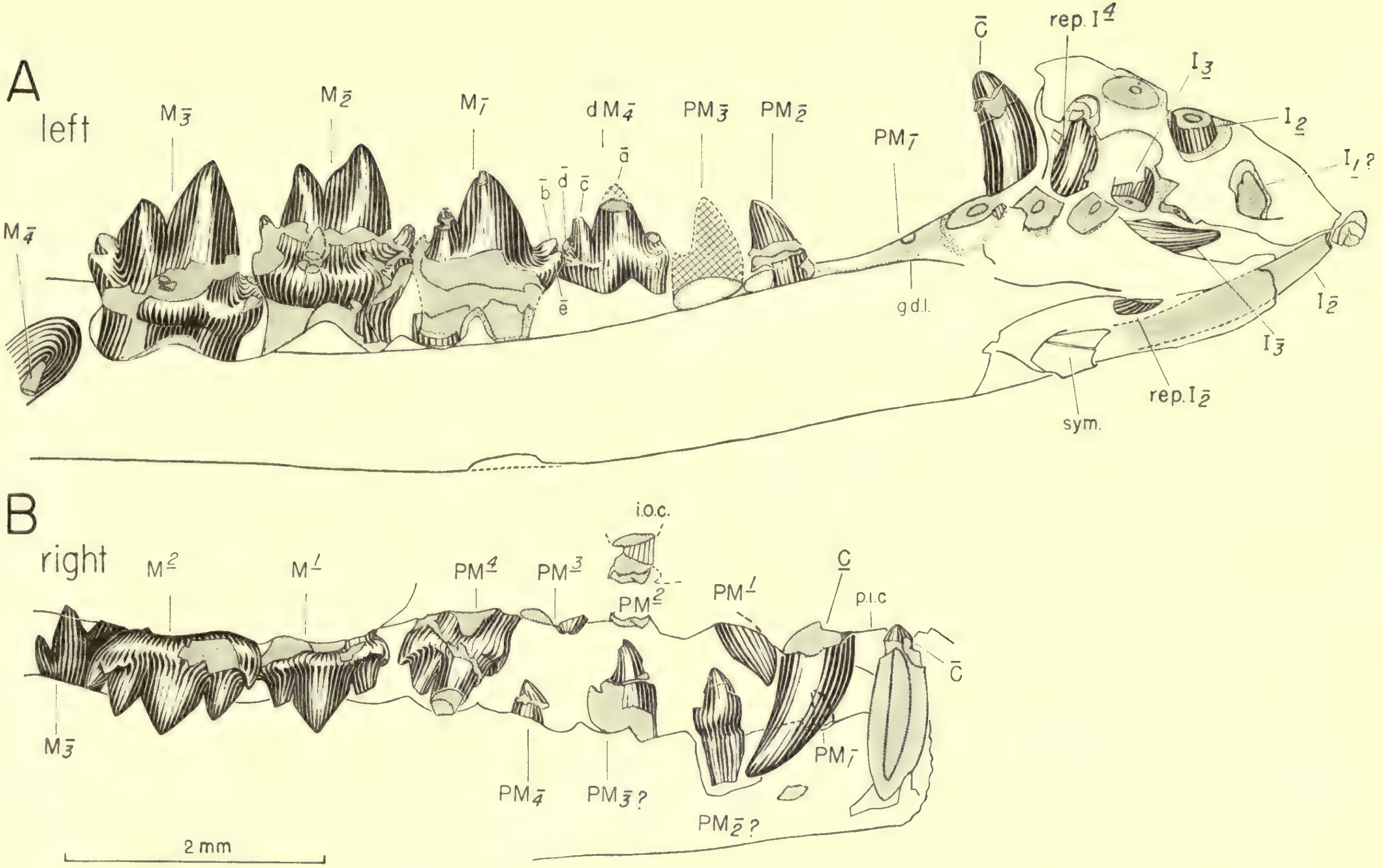
A
left
M4
M3
M2
M1
dM4
b
d
c
a
e
PM3
PM2
PM1
g.d.l.
C
rep. I4
I3
I2
I1?
I2
I3
rep. I2
sym.
B
right
M2
M1
PM4
PM3
i.o.c.
PM2
PM1
C
p.l.c
C
M3
PM4
PM3?
PM2?
PM1
2 mm

FIG. 1. *Erythrotherium parringtoni*. A. Internal view of the left dentary. B. External view of canine and postcanine dentitions on the right side. Abbreviations used in this and subsequent figures:

a. PM$_{\bar{1}}$	Alveolus of the first premolar	pa	Paracone	r. PM$^{\underline{3}}$	Replacing third upper premolar
c.e.	Cutting edge	p.l.c.	Palatal pit for lower canine	rep. I	Replacing incisor
g.d.l.	Groove for dental lamina	pr	Protocone	sh.p.	Shearing plane
i.o.c.	Infraorbital canal	pr^{d}	Protoconid	sty	Stylocone
me^{d}	Metaconid	p.u.p.c.	Pit for upper postcanine	sym	Symphysis

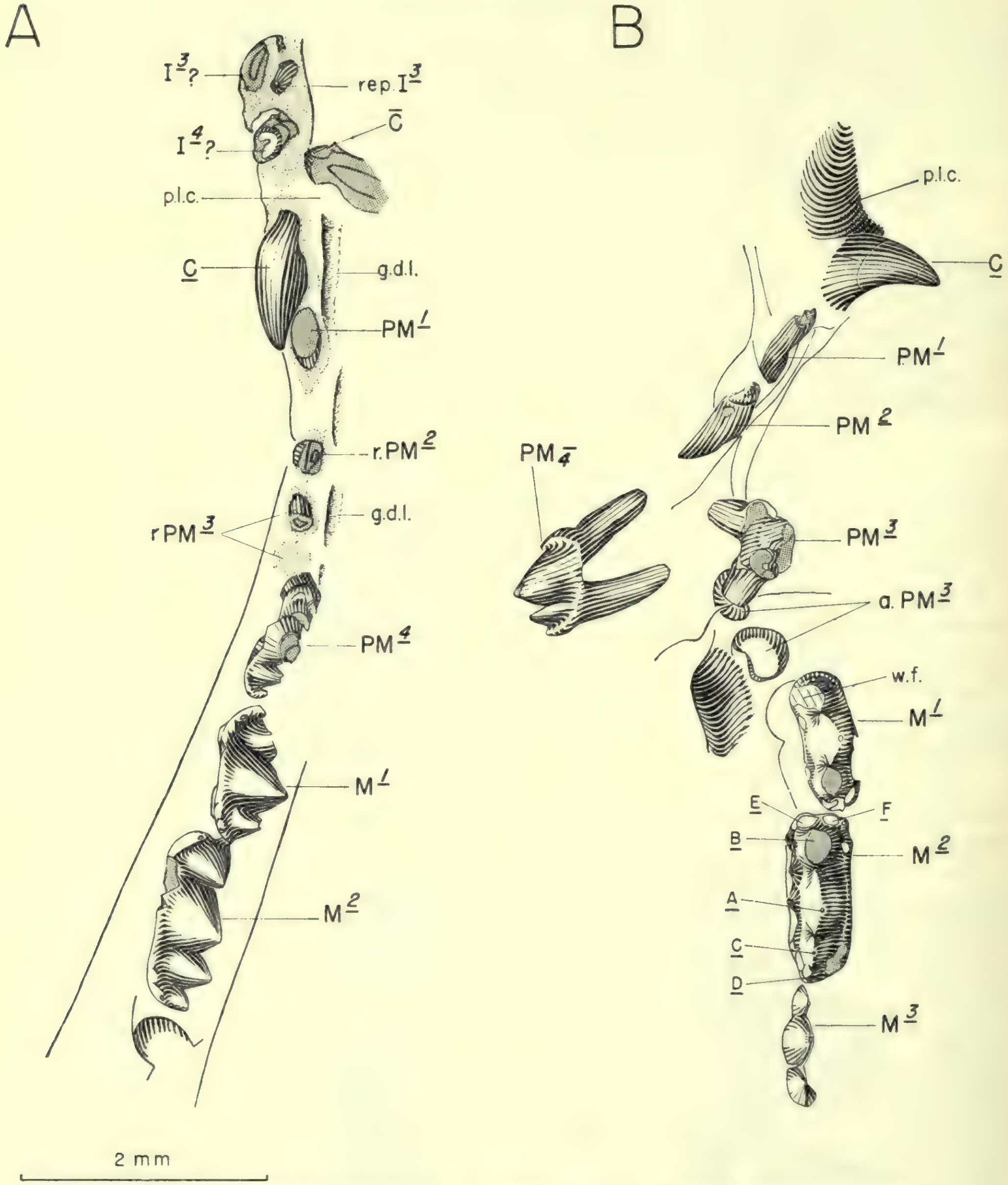
A
B
I^3?
rep. I^3
$\bar{C}$
I^4?
p.l.c.
$\underline{C}$
g.d.l.
PM^1
r.PM^2
g.d.l.
rPM^3
PM^4
M^1
M^2
p.l.c.
$\underline{C}$
PM^1
PM^2
$PM_{\bar{4}}$
PM^3
a. PM^3
w.f.
M^1
$\underline{E}$
$\underline{F}$
$\underline{B}$
M^2
$\underline{A}$
$\underline{C}$
$\underline{D}$
M^3
2 mm

FIG. 2. *Erythrotherium parringtoni*. Crown views. A. Right upper dentition. B. Left upper dentition. (See Text-fig. 1 for abbreviations.)

multituberculates and monotremes) (Kermack 1967; Kermack & Kielan-Jaworowska 1971) whereas the Kuehneotheriidae are related to the therian mammalian radiation (including the Orders Pantotheria and Symmetrodonta (*sensu* Simpson 1945, 1971) as well as the Infraclasses Eutheria and Metatheria).

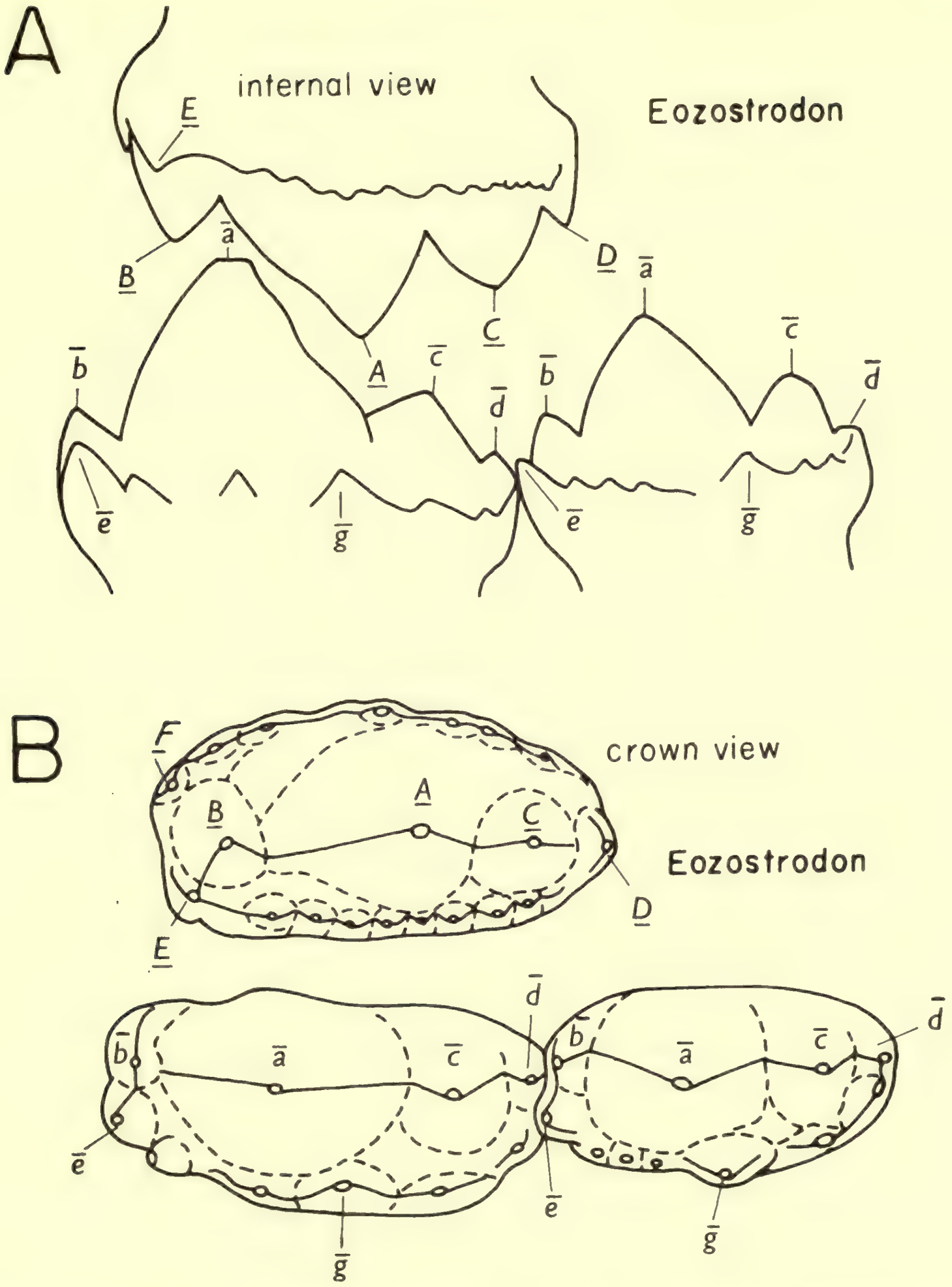
A
internal view
Eozostrodon
$\underline{E}$
$\underline{B}$
$\bar{a}$
$\underline{D}$
$\bar{a}$
$\underline{C}$
$\underline{A}$
$\bar{c}$
$\bar{b}$
$\bar{d}$
$\bar{b}$
$\bar{c}$
$\bar{d}$
$\bar{e}$
$\bar{g}$
$\bar{e}$
$\bar{g}$
B
crown view
$\underline{F}$
$\underline{B}$
$\underline{A}$
$\underline{C}$
Eozostrodon
$\underline{D}$
$\underline{E}$
$\bar{d}$
$\bar{d}$
$\bar{b}$
$\bar{a}$
$\bar{c}$
$\bar{b}$
$\bar{a}$
$\bar{c}$
$\bar{e}$
$\bar{e}$
$\bar{g}$
$\bar{g}$

FIG. 3. *Eozostrodon parvus*. A. Internal, and B. Crown view of upper and lower molars to illustrate the positions of the cusps lettered $\bar{a}$ to $\bar{g}$ in the lower molars, and $\underline{A}$ to $\underline{F}$ in the upper molars. The same letters have been used in the description and illustration of the molars of *Erythrotherium parringtoni* and *Megazostrodon rudnerae*.

Conflicting views on the closeness of the relationship between the Kuehneotheriidae and Morganucodontidae (including *Eozostrodon, Sinoconodon, Erythrotherium* and *Megazostrodon*) have been published. The problem has recently been admirably reviewed by Clemens (1970). Parrington (1971, 1973), Crompton & Jenkins (1968), Hopson & Crompton (1969) and Hopson (1969) have suggested that a close relationship existed between these two families and that both could have been derived from a galesaurid (= thrinaxodontid) cynodont of early to middle Triassic age.[3] *Probainognathus jenseni* (Romer 1969, 1970) from the middle Triassic of South America could well be, as has been suggested by Romer, a representative of the cynodont group from which mammals arose. *Probainognathus* is not highly specialized and the structure of the jaw articulation (Crompton 1972a), the structure of the postcanines, the tooth replacement pattern, the postcanine occlusion and the structure of the side wall of the braincase do not appear to debar it from being related to early mammals. Mills (1971), Kermack (1967) and Kermack & Kielan-Jaworowska (1971) are of the opinion that the differences between the two main groups of early mammals indicate that they are not closely related. If the ancestral stock from which the recognized orders of Triassic and Jurassic mammals arose did not lie close to the mammal–reptile boundary, it implies that many of the features which were not present in the ancestral group but which are common to both therian and non-therian mammals must have evolved independently in parallel in the two main phyletic lines. If, on the other hand, it is shown that a close relationship did exist between the Morganucodontidae and the Kuehneotheriidae, this imples that few of the mammalian osteological features (and, by implication, physiological features as well) evolved independently in parallel in the two lines.

The different phyletic lines of cynodonts are characterized by parallel acquisition of mammalian features and it is obvious that some of the common features of later non-therian and therian mammals (for example, the mammalian three-boned middle ear) must have evolved independently in these two groups (Hopson 1966). If it can be confirmed that the Kuehneotheriidae and the Morganucodontidae lay at the base of the two main mammalian radiations, and if they are shown to be closely related, it will mean that the line separating the therapsid and mammalian radiations can be more precisely drawn than was previously the case. It is well known that discrete characters previously thought to be diagnostic of mammals, such as the squamoso-dentary articulation, arose independently on more than one occasion (see Barghusen & Hopson 1970; Crompton 1972a) and this necessitates basing the diagnosis of what constitutes a mammal on a mosaic of several characters (Hopson & Crompton 1969; Hopson 1970).

The conflicting views of the origin of therian and non-therian mammals are at present based principally upon interpretation of the structure of the dentition and of the lateral wall of the braincase. In this paper the dentitions of the known Triassic mammals (excluding the Haramiyidae) will be discussed with reference to this problem and it is hoped in a later paper to review the structure of the braincase in therapsids and early mammals.

---

[3] The haramiyids may prove to be related to both the eozostrodontids and the multituberculates (Hahn 1969).

II. DENTITION OF *ERYTHROTHERIUM PARRINGTONI*

(Text-figs. 1–3, Pl. 1)

A general description of the lower dentition of *Erythrotherium parringtoni* has already been given (Crompton 1964; Crompton & Jenkins 1968) so that it is not necessary to repeat that here.

This discussion will concentrate instead on additional details exposed by further preparation of the type specimen. The type is an immature animal in which some of the milk teeth were still functional.

Lower dentition

In the earlier description of the left mandible, a small pit was described behind the functional canine and it was suggested that this was the remnant of the root of an anterior postcanine tooth (Text-fig. 1A, $PM_{\bar{1}}$). It now can be seen that the partially erupted tip of a tooth is present in the same position in the right mandible (Text-fig. 1B, $PM_{\bar{1}}$). This appears to be a partially erupted first premolar. The pit in the left mandible lies in the groove for the dental lamina (Text-fig. 1A, g.d.l.) and it is concluded that the left first premolar would have erupted in this position later in life and that the preceding milk molar was shed shortly before death. The fifth and sixth postcanines ($M_{\bar{1}}$ and $M_{\bar{2}}$) on the left are fully erupted and are considerably larger than the fourth postcanine ($dM_{\bar{4}}$). The fourth lower postcanine on the right (Text-fig. 1B) is only partially erupted and is identified as the fourth premolar ($PM_{\bar{4}}$). The fifth, sixth and seventh lower postcanines ($M_{\bar{1}}$ to $M_{\bar{3}}$) are almost identical in structure to the molars of *Eozostrodon parvus*; it is concluded that they are the first, second and third molars. The fourth postcanine ($dM_{\bar{4}}$) on the left is almost identical in crown structure to the molar teeth behind. This is in sharp contrast to the situation in *Eozostrodon* where the ultimate premolar is markedly different in size and form from the first molar. This suggests that it is a milk molar (see Parrington 1971, pl. 45, fig. D). The posterior accessory cusp,[4] or cusp $\bar{d}$, of the fourth milk molar (Text-fig. 1A) fits into a shallow embayment between cusps $\bar{b}$ and $\bar{e}$ on the anterior surface of the first molar, forming a tongue-in-groove junction. The last milk molar and first molar lack Kühnecones (cusp $\bar{g}$). This area is extensively damaged on $M_{\bar{1}}$ on the left side but is well preserved on the right (not figured). The Kühnecones of $M_{\bar{2}}$ and $M_{\bar{3}}$ are large. $M_{\bar{4}}$ is only partially erupted and partially formed. The root of the second premolar on the right side is partially exposed; Mills (1971) has also found single-rooted second premolars in *Eozostrodon*. The crown of the third premolar was lost during recent preparation of the specimen and, unlike *Eozostrodon*, this tooth appears to be single-rooted, but it is not possible to establish beyond doubt that the second and third postcanines of *Erythrotherium* are premolars rather than molars.

---

[4] In order to simplify the description of the postcanines, cusps will be referred to by the letters which were used in our previous discussion and description (Crompton & Jenkins, 1968; see Text-fig. 3 here). The cusps of upper teeth are indicated by capital letters with a line below (e.g. $\underline{A}$) and cusps of lower teeth by lower case letters with a line above (e.g. $\bar{a}$). Parrington has referred to the prominent cingulum cusp ($\bar{g}$) of the lower molars as the Kühnecone and this term will be used in this paper.

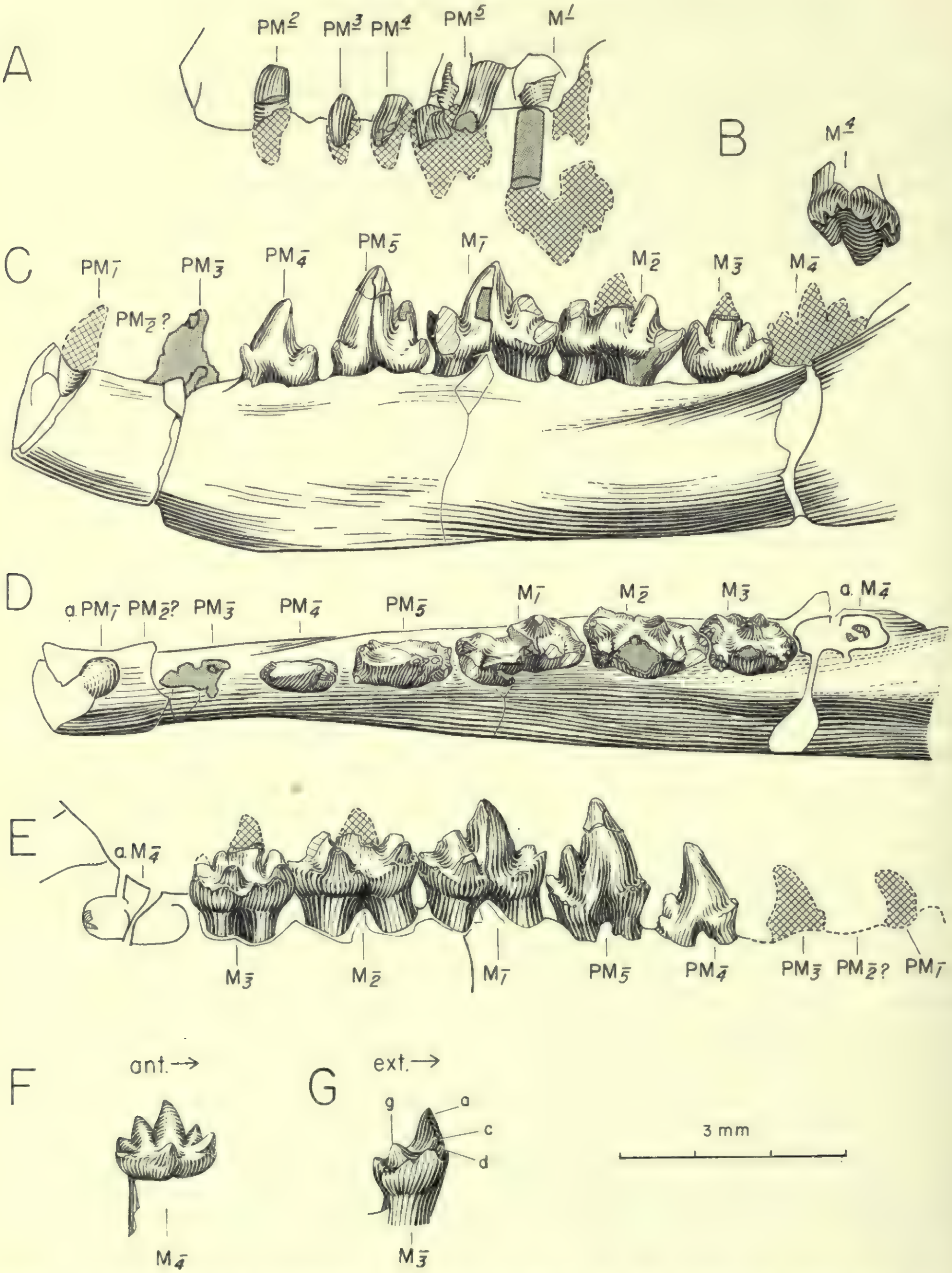
A
PM2
PM3
PM4
PM5
M1
B
M4
C
PM1
PM2 ?
PM3
PM4
PM5
M1
M2
M3
M4
D
a. PM1
PM2?
PM3
PM4
PM5
M1
M2
M3
a. M4
E
a. M4
M3
M2
M1
PM5
PM4
PM3
PM2?
PM1
F
ant. →
M4
G
ext. →
g
a
c
d
M3
3 mm

FIG. 4. *Megazostrodon rudnerae.* A. External view of the preserved portion of the upper left dentition. B. External view of isolated left M^4. C. External view of left lower premolar–molar dentition. D. Crown view of the same. E. Internal view of the same. F. Isolated lower left M_4. G. Posterior view of right lower M_3.

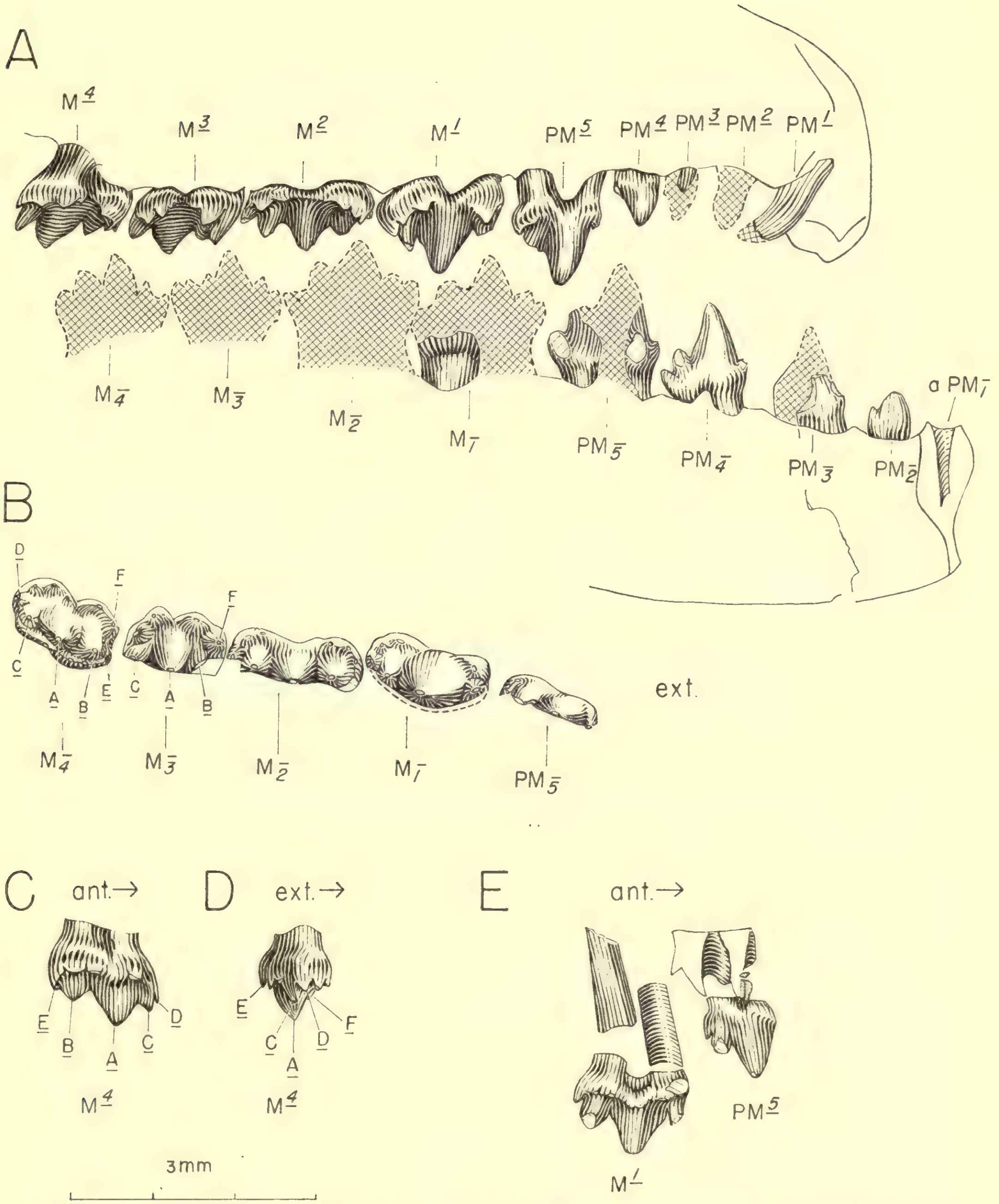
A
M^{4}
M^{3}
M^{2}
M^{1}
PM^{5}
PM^{4}
PM^{3}
PM^{2}
PM^{1}
M_{4}
M_{3}
M_{2}
M_{1}
PM_{5}
PM_{4}
PM_{3}
PM_{2}
a PM_{1}
B
D
F
C
A
B
E
C
A
B
F
M_{4}
M_{3}
M_{2}
M_{1}
PM_{5}
ext.
C
ant.→
E
B
A
C
D
M^{4}
D
ext.→
E
C
A
D
F
M^{4}
E
ant.→
PM^{5}
M^{1}
3mm

FIG. 5. *Megazostrodon rudnerae.* A. External view of right dentition. Outlines of the lower teeth based on a medial view. B. Crown view of last premolar and molars of right side. C. Medial view of right upper M^{4}. D. Posterior view of the same. E. Internal view of left PM^{5} and M^{1}.

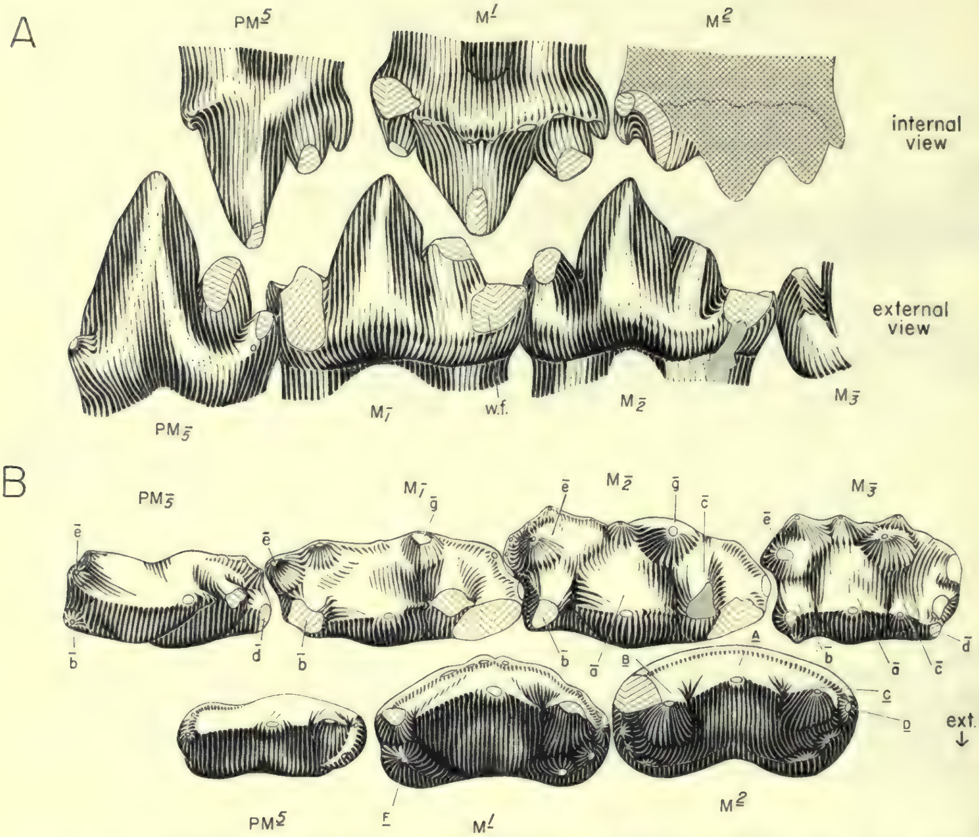

Fig. 6. *Megazostrodon rudnerae*. Reconstruction of postcanine occlusion. A. Internal view of upper PM^5–M^2 and external view of corresponding lowers. B. Crown view of upper PM^5–M^2 and lower PM$_5$–M$_3$.

Upper dentition

The upper incisor region is not well preserved. On the left it is partially exposed by a fracture through the left premaxilla (Text-fig. 1A) and on the right only the last two damaged incisors are in position (Text-fig. 2A). There are at least four upper incisors. The ultimate incisor on the left and the penultimate incisor on the right have replacing incisors internally at their bases (rep. I). A partially erupted PM^1 lies directly behind each of the functional upper canines (Text-figs. 1B, 2). The tips of these are directed forward and appear to touch the base of the functioning canine. This suggests that they may be replacing canines, but Parrington (1972, fig. 7) has shown that in *Eozostrodon* a replacing upper canine lies medial to the functional canine. For this reason, it is concluded that these erupting teeth are the first permanent premolars. A groove for the dental lamina lies in the maxilla medial to the functional canine and is confluent with the alveolus of the erupting first premolar (Text-fig. 2A, g.d.l.). Antero-medial to the upper functional canine, a shallow pit (p.l.c.) is present in the palate (Text-figs. 2A, 2B). This accommodates the tip of the lower canine and is similar to the pit in the palate of *Eozostrodon parvus*, cynodonts, and several other therapsid groups. The second upper premolar is preserved only on the left (Text-fig. 2B) ; it is a single-rooted tooth with a small posterior heel on the crown. The third premolar is also only preserved on the left. It is a double-rooted tooth with a tricuspid crown and a small heel behind the posterior cusp. The fourth premolars are preserved on both sides (Text-figs. 1B, 2) ; the right one is *in situ* and that on the left is displaced but preserved in the matrix near its alveolus. The crown is dominated by a main cusp having its anterior border considerably longer than its posterior. A small anterior cusp is present and is closer to the base of the tooth than the small cusp which lies posterior to the main cusp. Cusp $\underline{\mathrm{C}}$ is followed by a smaller cusp $\underline{\mathrm{D}}$. A faint cingulum is present on the antero-external and postero-external surfaces of the crown. The tips of the roots are not expanded, but this does not necessarily invalidate a close relationship between *Erythrotherium* and *Eozostrodon.* Parrington (1973) pointed out that the expansion of the tips of the molar and premolar roots in *Eozostrodon* is a feature developed in mature specimens.

The first molar is preserved *in situ* on both sides (Text-fig. 1B, 2). It is considerably larger than, and differs markedly from, the fourth premolar. The anterior border of the main cusp $\underline{\mathrm{A}}$ is longer than the posterior, but the discrepancy is not as marked as in the fourth premolar. Cusp $\underline{\mathrm{B}}$ is larger than that of the fourth premolar ; a slightly cuspidate cingulum is confined to the anterior and posterior regions of the tooth and a faint cingulum is present along the entire internal surface. The tip of cusp $\underline{\mathrm{B}}$ has been worn down (w.f.) forming an oblique facet facing downward and inward (Text-fig. 2B).

The second molar (Plate 1, Text-figs. 1B, 2) is the largest of the preserved teeth. Cusps $\underline{\mathrm{B}}$ and $\underline{\mathrm{C}}$ are, relative to cusp $\underline{\mathrm{A}}$, larger than in the first molar. The front of the tooth is broad and supports two small cusps ($\underline{\mathrm{E}}$ and $\underline{\mathrm{F}}$) with a slight embayment between them. This, together with cusp $\underline{\mathrm{D}}$ of the first molar, forms a junction between the two molars not unlike that described for the lowers. The external cingulum is poorly developed. The partially formed and partially erupted crown of the third molar is present on the left but this tooth is not preserved on the right. The spacing between the tips of the main cusps is less than in the second molar so that when fully formed this tooth would have been smaller than the second molar.

The dental formula for *Erythrotherium parringtoni* appears to be : $\mathrm{I}\frac{4+?}{3+?}\,\mathrm{C}\frac{1}{1}\,\mathrm{PM}\frac{4}{4}\,\mathrm{M}\frac{3+?}{4}$. In the type specimen, the erupting first premolar lies directly behind the canine and there is therefore no evidence that five teeth (premolars or milk molars) were present in a less mature specimen.

On the basis of a study of the morphology of numerous molar teeth, Mills (1971) has correctly pointed out that *Erythrotherium parringtoni* and *Eozostrodon parvus* are almost identical and that the distinctions which I had previously listed (1964) are no longer valid reasons for placing the African form in a separate genus because all the features of *Erythrotherium* molars are encountered in a large sample of *Eozostrodon* molars. However, there are reasons for retaining the southern African form in a separate genus. In *Eozostrodon* (Parrington 1971, 1972 ; Mills 1971) the first upper molar is the same size or even slightly smaller than the ultimate premolar. Mills (1971 : 34) has stated that the ultimate premolar '. . . is as long as the longest molar and rather higher'. In *Erythrotherium*, on the other hand, the ultimate upper premolar is smaller than the first molar ; this may be a characteristic of the southern African eozostrodontids (see discussion of *Megazostrodon* below). In the lower jaw of *Erythrotherium*, the last premolar is only partially erupted and its crown structure is not known and so cannot be compared with *Eozostrodon*. In *Erythrotherium*, the Kühnecone is absent on the first lower molar whereas in *Eozostrodon parvus* it is present.

The number of partially formed, partially erupted and replacing teeth establishes beyond doubt that the type of *Erythrotherium* was a young animal. For this reason it is not possible to determine the occlusal pattern. However, wear on M^1 suggests that when the jaws were closed, the main cusp ($\bar{a}$) of the lower molar lay anterior to the cusp $\underline{B}$ of an upper molar rather than behind it as is the case in *Eozostrodon*. A similar situation to that of *Erythrotherium* has been described for *Megazostrodon* and this is discussed further on p. 415.

III. THE DENTITION OF *MEGAZOSTRODON RUDNERAE*

(Text-figs. 4–6, Pls. 1, 2)

Preliminary descriptions of the dentition of *Megazostrodon rudnerae* have been given in previous papers (Crompton & Jenkins 1968 ; Hopson & Crompton 1969). Subsequently the skull of the type has been further prepared as extensively as possible without endangering the specimen.

Lower dentition

It is difficult to be certain about the number of lower premolars because the incisors and canine are not preserved. There appear to be four premolars on the left (Text-fig. 4), and five on the right (Text-fig. 5A). The first premolar is represented by the posterior rim of an empty alveolus (a. $PM_{\bar{1}}$) on both sides. It is possible that this is the remnant of a canine alveolus rather than a premolar alveolus. If this proves to be the case, the premolar count would be four instead of five and the canine would have been a very small tooth. The second premolar on the right is small with a minute posterior heel. The corresponding tooth is absent on the left and a small diastema separates the alveoli for the first premolar and the third premolar (Text-figs. 4, $PM_{\bar{2}}$?). There is no evidence in this diastema of a bony plug which would indicate the presence of a resorbed root. The third premolar is larger and has a slightly recurved main cusp and a small posterior heel. The fourth premolar is well preserved on both sides. A small cusp $\bar{b}$ is present in front of and at the base of the main cusp. A small cingulum runs posteriorly from this cusp on the inner side of the tooth. A larger cusp $\bar{c}$ lies at a higher level than cusp $\bar{b}$ immediately behind the main cusp $\bar{a}$. At a lower level and postero-medial to cusp $\bar{c}$ a minute cuspule $\bar{d}$ is present. The outline of the fifth lower premolar is almost identical to that of the fourth premolar (Text-figs. 4, 6), but there are some interesting differences. Two small cusps, $\bar{b}$ and $\bar{e}$, lying at approximately the same height are present on the front of the tooth at the base of the main cusp. They are separated by a shallow embayment. A short cingulum supporting a small cusp runs backward from cusp $\bar{e}$ on the internal surface of the tooth. A prominent cusp $\bar{c}$ lies behind the main cusp. A smaller cusp $\bar{d}$ lies behind and slightly on the external side. From this cusp, a cingulum supporting several cusps runs downward and forward on the internal surface of the crown. The most posterior cusp on this cingulum is at a slightly lower level that cusp $\bar{d}$ and the ridge connecting these two cusps is slightly concave. The external surface of cusp $\bar{e}$ of the first molars butts against this region of the fifth premolar. Wear is present on the external surface of the tips of cusps $\bar{c}$ and $\bar{d}$ (Text-fig. 6).

The first lower molar differs distinctly from the fifth premolar ; it is larger and has a prominent internal cingulum supporting a large Kühnecone (Plate 1). Cusp $\bar{a}$ is relatively less prominent than cusp $\bar{a}$ in the fifth premolar. The outer surface and tip of cusp $\bar{b}$ is fairly heavily worn (Text-fig. 6). Cusp $\bar{e}$ is a prominent feature of the crown and is far larger than in any of the other known eozostrodontids ; it projects further forward than cusp $\bar{b}$. Consequently, in external view, cusp $\bar{b}$ does not appear to be a small cingular cusp as it does in *Eozostrodon parvus* (Text-fig. 3) where it is relatively small and where cusp $\bar{e}$ is smaller than in *Megazostrodon*. A lingual cingulum runs backward for a short distance from cusp $\bar{e}$ and supports a small cuspule. The Kühnecone is extremely large and not connected by either ridges or cingula to the other cusps of the crown. The tip of cusp $\bar{c}$ is slightly worn, as is the outer surface of the tooth behind cusp $\bar{c}$ (Text-fig. 6, w.f.). A distinct cusp is not preserved and was obliterated by wear. The important point is that cusp $\underline{A}$ of the upper first molar (Text-fig. 6A) must have lain external to the gap between cusps $\bar{c}$ and $\bar{d}$ when the jaws were closed. A wider space separates the base of cusp $\bar{c}$ from the posterior margin of the tooth than is found in the typical lower molars of *Eozostrodon parvus*. In the crown view (Text-fig. 6B) this region is also narrower than in *E. parvus* where the posterior region of the crown of the lower molars is usually wider than the remainder of the crown (Text-fig. 3B). This region in *Megazostrodon* is reminiscent of a 'talonid' heel of early therian mammals such as *Kuehneotherium* (Text-fig. 7B).

The second molar of *Megazostrodon* is well preserved on both sides although on the right only the medial view is exposed. The crown structure is very similar to that of the first molar but there are differences. Cusp $\bar{e}$ is larger and more widely separated from cusp $\bar{b}$. The anterior border of cusp $\bar{e}$ lies further forward of cusp $\bar{b}$ than it does in the first molar. A wide embayment is present on the front surface of the crown between cusps $\bar{e}$ and $\bar{b}$. This receives the 'talonid' of the first molar (Text-fig. 6B). A prominent cingulum is present on the antero-internal surface of cusp $\bar{e}$. This cingulum is cuspidate with the largest cuspule postero-medial to cusp $\bar{e}$. Beyond this point it continues backward to the base of the Kühnecone where it is terminated by a cuspule. The tip of cusp $\bar{c}$ and the external surface of the tooth behind this cusp are worn and cusp $\bar{d}$ has been obliterated. A wide 'talonid' shelf separates the base of cusp $\bar{c}$ from the posterior margin of the tooth (Text-fig. 6A). On the left $M_{\bar{2}}$ the crown surface of the 'talonid' shelf appears to be worn but this does not appear to be the case for the corresponding tooth on the right (Plate 1). The posterior tip of the 'talonid' fits into a shallow embayment between cusps b̄ and ē of the third molar.

In crown view, the third molar is shorter and more bulbous than the second molar. Cusps b̄ and ē are large and a prominent cingular cusp is present internal to cusp ē, but this does not extend onto the anterior surface of cusp ē as is the case on the second molar. A striking feature of this tooth is the internal cingulum which extends without interruption from cusp ē to cusp d̄ and lies internal to the Kühnecone (Pl. 1). This cingulum supports six cuspules in addition to cusps d̄ and ē. A prominent cusp is present internal to the Kühnecone. Consequently the Kühnecone in this tooth would be defined not as an enlarged cingular cusp, as in the first and second molars of *Megazostrodon* or in the molars of *Eozostrodon parvus*, but as a crown cusp. In Text-fig. 4G the third lower molar as seen from behind is illustrated. This clearly shows the great width of the tooth medial to the main cusp (ā) and the cingular cusp outside the Kühnecone (ḡ). The cingula present antero-internal to cusp ē on the second molar and internal to the Kühnecone on the third molar illustrate how within one individual the same cusp can be defined either as a cingular or a crown cusp. Cusp c̄ of the third molar is minute and this clearly distinguishes this tooth from the other molars. Other than small wear facets on the tips of cusps b̄ and d̄, this tooth shows no signs of wear. A small cusp is present on the external surface of cusp b̄ (Text-fig. 6). In both right and left rami a double-rooted empty alveolus lies behind the third molar. The bones of the left side of the snout and the posterior part of the skull were macerated slightly before fossilization. Lying among these bones is an isolated molar. It has been identified as the fourth left lower molar (Text-fig. 4F) because it differs from the morphology of all the known upper molars ; it is the right size for the empty alveolus and it possesses a well-developed Kühnecone. Unfortunately, only the internal view and part of the external view of this tooth could be exposed. The tooth is similar to the first and second molars in having cusp c̄ larger than cusp b̄. This contrasts with the condition in the third lower molars. The internal cingulum is poorly developed. The third molar is 'odd man out' in that cusp c̄ is reduced, a cuspule is present on the external surface, and the Kühnecone has the appearance of a crown cusp rather than a cingular cusp. The marked difference between the third molar and the adjoining molars is also a feature of the upper dentition of *Megazostrodon*.

Upper dentition

As in the lower jaw, it is difficult to be certain about the number of premolars because an upper canine is not preserved. The first postcanine tooth preserved on the right side has been identified as the first premolar (Text-fig. 5A). Its tip is worn and its single root is partially exposed. It is followed by a gap that appears to contain the remnants of the root of the second premolar. On the left side (Text-fig. 4A) the root of the corresponding tooth and part of its alveolus are preserved. This is also a single-rooted tooth. The third premolar on both sides is represented by a worn nubbin of dentine. The fourth premolar on the right side is well preserved whereas that on the left is damaged. It consists of a main cusp followed by a small posterior heel near the base of the tooth. This tooth appears to be single-rooted.

The external surface of the fifth premolar is preserved on the right side (Text-fig. 5A) and the internal surface preserved on the left (Text-fig. 5E). The crown is dominated by a main cusp. A minute capsule is present in front at the base of the crown and two cusps, both larger than the anterior one, are present behind the main cusp. Of these, the first is larger. A small external cingulum runs forward from the posterior cusp and terminates above the gap between cusps $\underline{B}$ and $\underline{A}$. Unlike the first four premolars, this tooth is double-rooted. The external view of the first molar is also exposed on the right side (Text-fig. 5A), and the internal view on the left (Text-fig. 5E). The main cusp dominates the crown in this tooth and its anterior border is longer than the posterior, reflecting the discrepancy in size between cusps $\underline{B}$ and $\underline{C}$. A small cusp is present on the external surface of cusp $\underline{B}$. Cusp $\underline{C}$ is followed by a smaller cusp $\underline{D}$. A short external cingulum runs forward from $\underline{D}$ and supports two small cuspules. The anterior and posterior portions of the external cingulum do not meet and, consequently, in crown view the tooth is bean- or kidney-shaped (Text-fig. 6B). A narrow internal cingulum runs backwards from the base of cusp $\underline{B}$ to the tip of cusp $\underline{D}$. It is slightly crenulated and best developed above the tip of cusp $\underline{A}$ (Pl. 2). Oblique wear facets are present on the internal surface of the tips of cusps $\underline{B}$ and $\underline{C}$ and on the internal cingulum above cusps $\underline{C}$ and $\underline{B}$ (Text-fig. 6A). Poorly developed wear facets are also present on the internal surface of cusp $\underline{A}$ near the tip of this cusp and on the internal surface of the tooth immediately above cusp $\underline{B}$. The internal surface of the tooth is markedly convex in crown view and the three main cusps form an obtuse angle, rather than being in line. This is in contrast to the condition in M^{4}. Both of the roots of the left first molar were exposed by a fracture (Text-fig. 5E). These taper towards their tips and lack the characteristic 'club feet' of *Eozostrodon*. As all the molars of the type of *Megazostrodon* are fully erupted, it was presumably a mature individual. Expansion of the root tips is found only in mature individuals of *Eozostrodon* and the absence of this feature in *Megazostrodon* is a clear difference between the two genera.

M^{2} is characterized by the nearly equal development of the crown in front of and behind the main cusp so that $\underline{B}$ and $\underline{C}$ are nearly equal in height. A well-developed cingulum is present on the antero-external surface of the crown. This cingulum terminates above the gap between cusps $\underline{A}$ and $\underline{B}$ and supports three cuspules. The internal surface of cusp $\underline{B}$ is worn and if a cusp $\underline{E}$ were present, it has been obliterated by wear (this cusp is present on M^{4}). A well-developed and bulbous external cingulum runs forward from cusp $\underline{D}$ and terminates before reaching the midpoint of the tooth. Consequently, in crown view the tooth has the same bean-shaped appearance as M^{1}, except that it is slightly more pronounced. The internal surface of M^{2} could not be fully exposed. As in the first molar, the principal cusps are not in line. M^{3} is shorter and wider than M^{2} or M^{4}. The external cingulum is greatly enlarged and supports four distinct cuspules, two anterior to the midpoint and two posterior to the midpoint. Of these, the anterior cusp $\underline{F}$ (Text-fig. 5B) is the largest and it is larger than cusp $\underline{B}$. It is followed by a smaller cusp. The two postero-external cusps are sharply pointed and smaller than the anterior. Cusp $\underline{D}$ is absent and the external cingulum terminates at the base of cusp $\underline{C}$. Immediately above the tip of the main cusp, the external cingulum is absent so that a V-shaped valley

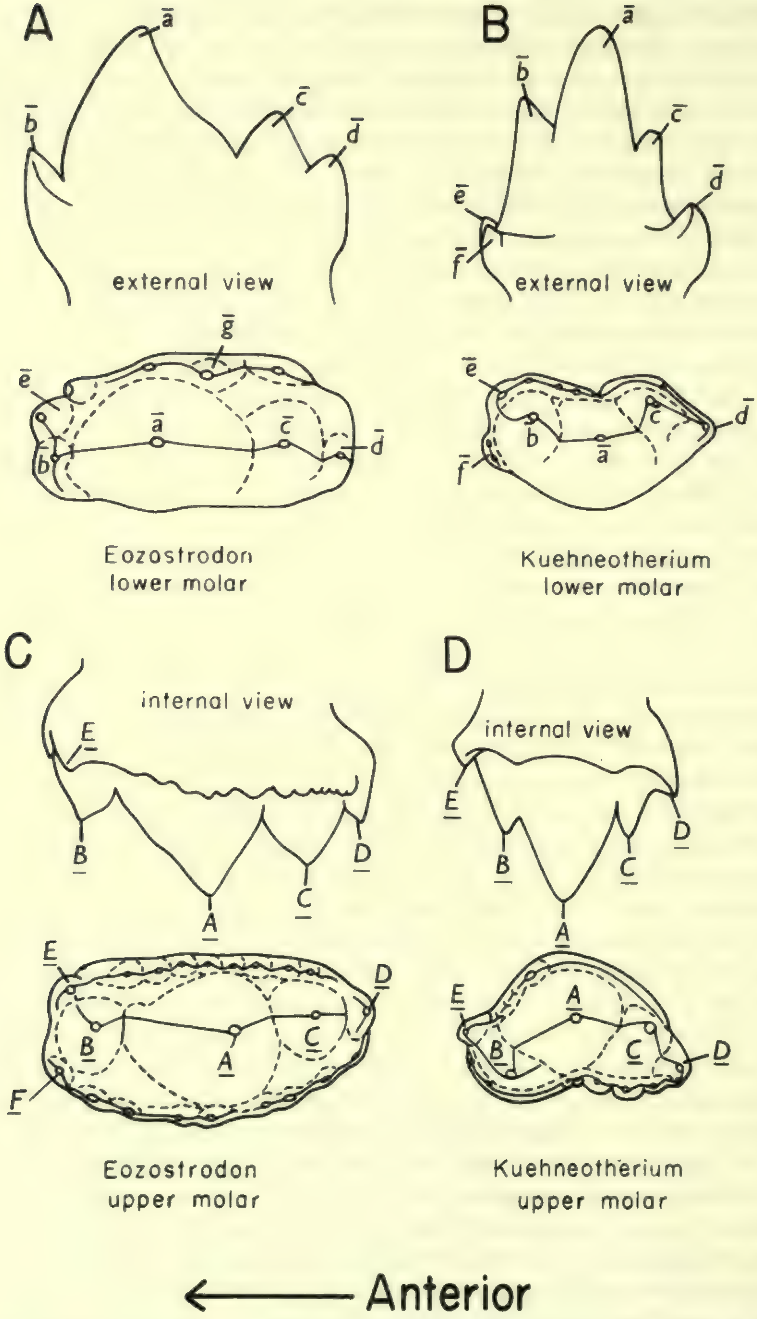
A
B
C
D
external view
external view
internal view
internal view
Eozostrodon
lower molar
Kuehneotherium
lower molar
Eozostrodon
upper molar
Kuehneotherium
upper molar
ā
b̄
c̄
d̄
ē
f̄
ḡ
A
B
C
D
E
F
Anterior

Fig. 7. Comparison of the upper and lower molars of *Kuehneotherium* and *Eozostrodon*.

separates the anterior and posterior portions of the external cingulum. Because of the large size of the cingulum and cingular cusps, prominent antero-lateral and postero-lateral basins separate the base of the main cusps from the cingular cusps. The antero-internal edge of the crown in front of cusp B̲ is heavily worn. The fourth upper molar is longer and narrower than M^3. The external cingulum is well developed and supports four large cusps separated by a V-shaped valley at the mid-point of the tooth. A small cusp D̲ is present. A marked feature of M^4 is that the tip of the main cusp lies behind the midpoint of the external surface (this is noticeable to a lesser extent in M^3 in Text-fig. 5A). M^4 is preserved on both sides (Text-figs. 4B, 5A); consequently this feature does not appear to be due to postmortem crushing. Part of the medial view of the right M^4 is exposed (Text-fig. 5C). A well-preserved cusp E̲ is present and a shallow embayment is present between this cusp and the antero-external cingular cusp F̲ (Text-fig. 5B). This embayment presumably accommodated the posterior surface of M^3. A narrow internal cingulum runs from cusp E̲ to the base of cusp C̲ (Text-fig. 5C). It supports four minor cuspules. The tips of these show some wear. In Text-fig. 5D, a posterior view of the fourth upper molar is shown. It illustrates the relative width of the internal and external cingula.

IV. MOLAR OCCLUSION

Widely differing opinions of the relationship between the two best known families of Triassic mammals, the Morganucodontidae and the Kuehneotheriidae, have been published. Mills (1971 : 49), basing his conclusions principally on the structure of the postcanine teeth, stated that the common ancestor of these two families must be placed '... some way below the mammalian level; they may well have evolved from different groups of mammal-like reptiles'. He also stated (*ibid.* : 49) that '...their teeth seem almost as unlike as one could imagine'. On the other hand, Parrington (1967, 1971, 1973), Crompton & Jenkins (1967, 1968) and Hopson &

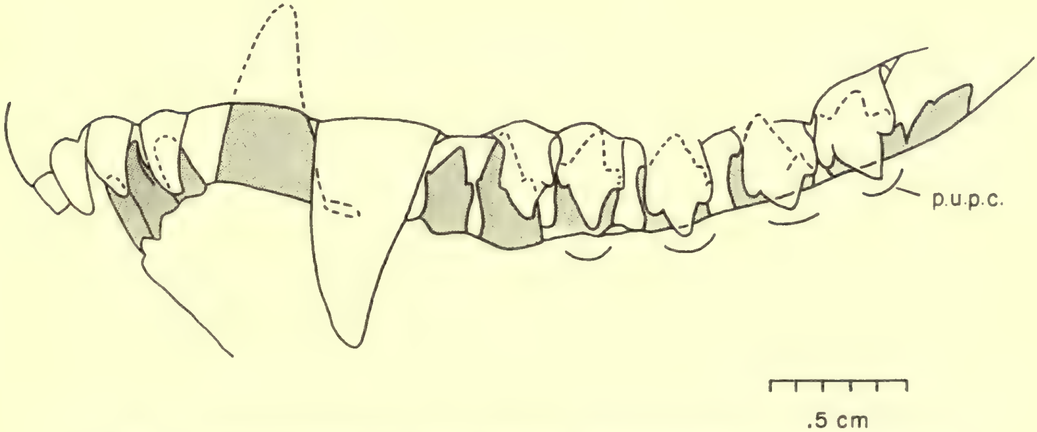

FIG. 8. *Thrinaxodon liorhinus*. Lateral view of the left side of the dentition.

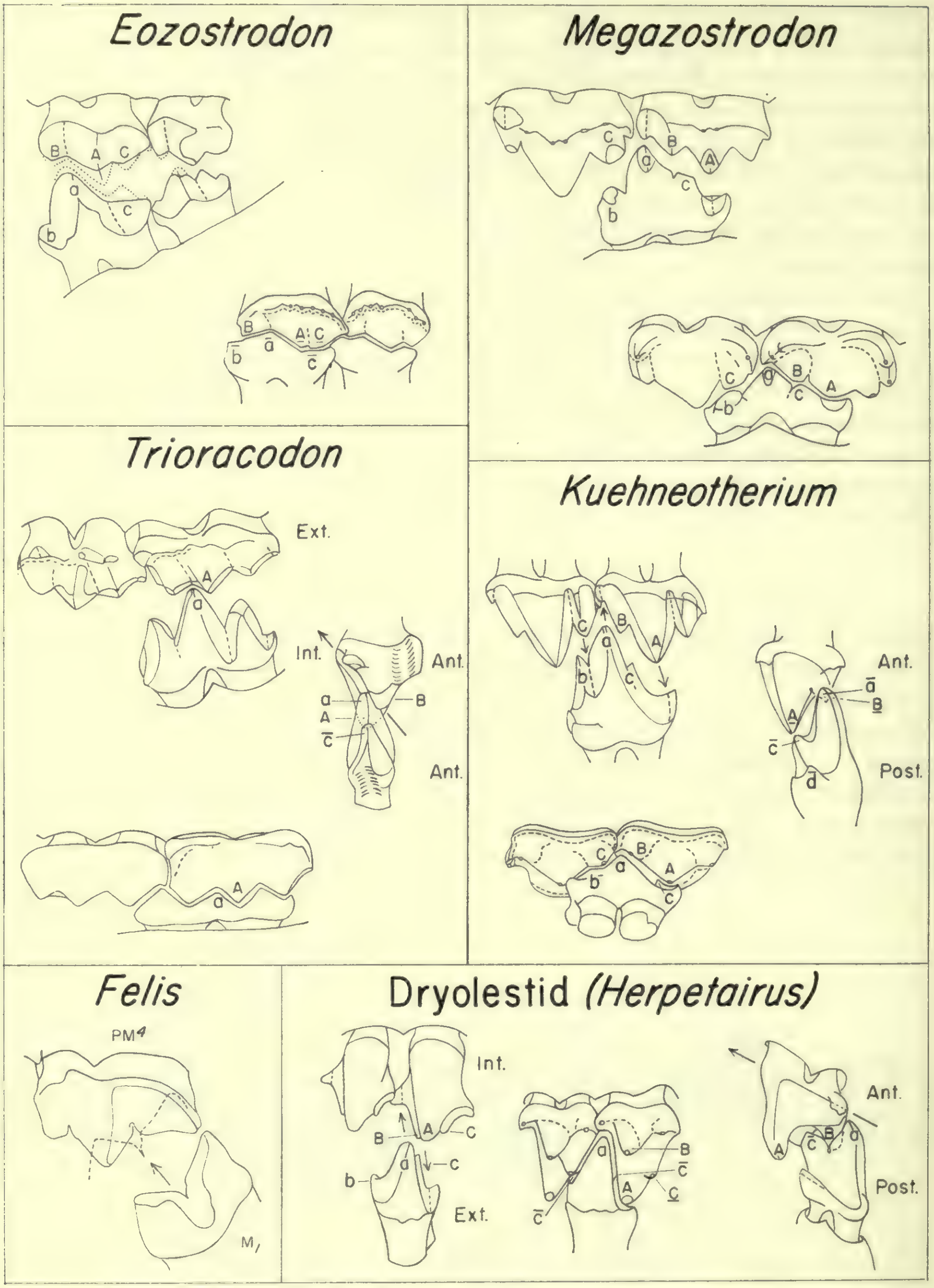
Eozostrodon
B
A
C
a
c
b
B
ā
A
C
b̄
c̄
Megazostrodon
C
B
A
a
c
b
C
a
B
A
c
b
Trioracodon
Ext.
A
a
Int.
Ant.
a
A
c̄
B
Ant.
A
a
Kuehneotherium
C
B
a
A
b
c
Ant.
ā
B
A
c̄
d̄
Post.
C
B
a
A
b̄
c̄
Felis
PM4
M1
Dryolestid (Herpetairus)
Int.
B
A
C
b
a
c
Ext.
a
B
c̄
A
C
c̄
Ant.
A
C
B
a
Post.

Fig. 9. Diagram illustrating the relative positions of upper and lower molars in a series of Mesozoic mammals and the carnassials of *Felis* sp. *Eozostrodon parvus*, internal view of two upper and external view of two lower molars to illustrate relative positions of occluding molars and an oblique view of the same two molars in occlusion as seen from

Crompton (1969) concluded that the structure and function of the postcanine teeth in the two families are so similar that they were probably closely related. These opposing views are in part based on the differing interpretations of the occlusal pattern in the two groups. Therefore, before discussing the relationships of *Megazostrodon* and *Erythrotherium*, a brief discussion of occlusion in early mammals is pertinent.

In primitive cynodonts such as *Thrinaxodon*, the inner surface of the upper and the external surface of the lower postcanine teeth did not come into contact during occlusion. A narrow space separated the upper and lower postcanine dentitions when the jaws were closed (Crompton & Jenkins 1968, fig. 10). This conclusion is based on a near perfect skull of *Thrinaxodon* completely freed from the matrix by acid. Matching wear facets on the postcanine teeth are absent and therefore during mastication the external surfaces of the lower postcanines were not forced against the internal surfaces of the upper postcanines. The function of these teeth was apparently simply to puncture and tear food. In *Thrinaxodon* the relative positions of upper and lower postcanines varied in different specimens. In the skull illustrated in Text-fig. 8, upper teeth lay directly external to the lower teeth when the jaws were closed. The positions of upper and lower postcanines relative to one another are indicated by shallow pits on the outer surface of the dentary (Text-fig. 8, p.u.p.c.) and on the ventral surface of the maxilla medial to the upper postcanines. Similar pits in the maxilla of *Eozostrodon* have been figured by Parrington (1971). In contrast to the skull illustrated in Text-fig. 8, other specimens of *Thrinaxodon* have upper and lower postcanines alternating with one another.

Thrinaxodon is characterized by alternate tooth replacement and small cusps on the posterior and anterior surfaces of adjoining teeth forming a 'tongue-in-groove' relationship to align the teeth accurately do not exist. Alternate tooth replacement would rule out precise occlusal relationships of the type seen in mammalian molars and the postcanines of some therapsids (Crompton 1972b). In these forms, either the topography of the crowns of the occluding teeth is such that they inherently have accurately matching surfaces or wear resulting from occlusion produces consistent, accurately matching surfaces on specific teeth.

In *Eozostrodon parvus*, Mills (1971) showed that the positions of upper and lower molars relative to one another are the same in all the specimens he studied. Consequently consistent wear facets are produced on molar teeth. As would be expected from this kind of occlusion, the molar teeth are added successively, are not replaced alternately, and small cusps form 'tongue-in-groove' junctions between adjoining molars. It has been shown (Crompton & Jenkins 1968; Parrington 1971; Mills

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a ventro-lateral position parallel to the plane of the shearing surfaces. *Megazostrodon rudnerae*, same views of M^1 and M^2 and M$_{\bar{1}}$. *Trioracodon*, same views plus an anterior view of two molars at the beginning of active occlusion. *Kuehneotherium*, same views. The anterior view of the upper and posterior view of the occluding teeth illustrate the single shearing surface above cusps $\underline{A}$ and $\underline{B}$ of the upper molars and below cusps $\bar{a}$ and $\bar{c}$ of the lower. Dryolestid, same views. *Felis* sp., external view of M$_{\bar{1}}$ and internal view of PM^4 to illustrate that the shearing mechanism of the carnassials is the same as that of the principal shearing surfaces in therian molars.

1971; Butler 1972) that in *Eozostrodon* when the jaws were closed, the main cusp ā of the lower molars lay external to the gap between cusp B̲ and cusp A̲ of the upper molars (Text-fig. 9, Pl. 3). The main cusp of the uppers (A̲) lay external to the gap between cusp ā and c̄ of the lowers. As a result of the lowers being pressed against the uppers during occlusion, deep wear facets were produced in the areas between the principal and subsidiary cusps to accommodate the principal cusps of the occluding molars. It therefore appears, as has been suggested by Mills (1971), that the gap between cusp A̲ and B̲ of the uppers and cusp ā and c̄ of the lowers determined the position of upper and lower postcanines relative to one another. However, as has already been pointed out (Crompton & Jenkins 1969; Parrington 1971) when wear commenced, the principal cusp of the lower molar only contacted the inner cingulum of the upper and the principal cusp of the upper only the outer external surface of the lower (see Crompton & Jenkins 1968, figs. $4A_1$ and C_1). It is only when wear became more extensive that it extended into the area between the principal cusps and subsidiary cusps. At this stage pronounced wear facets are present on the sides of the principal and subsidiary cusps. Consequently the topography of the crowns of the molars of *Eozostrodon* did not determine the initial contact points between occluding upper and lower molars. This concept is central to the difference of opinion concerning the relationship of the Morganucodontidae and the Kuehneotheriidae. In *Megazostrodon* (Text-fig. 9) which has molars in which the spacing of the three crown cusps, B̲, A̲ and C̲ and b̄, ā and c̄, is almost identical to that of *Eozostrodon*, the relative positions of upper and lower postcanines are different. This would not have been the case if the spacing of the cusps determined the relative positions of upper and lower teeth. In *Eozostrodon parvus*, efficient shearing between opposing molar teeth was not possible until wear had produced matching shearing surfaces. In order for these surfaces to be formed consistently in the same positions, the fixing of the relative positions of upper and lower postcanines and the substitution of a mammalian type of tooth replacement for the reptilian alternate tooth replacement was necessary. As shearing planes are only present on worn teeth, there must have been some additional fundamental, but as yet unrecognized advantage to fixing the relative positions of upper and lower molars.

In triconodonts (Text-fig. 9, *Trioracodon*), the relative positions of upper and lower molars are the same as those of *Eozostrodon parvus* (Mills 1971); detailed study of the wear pattern in American Jurassic triconodonts has confirmed Mills' findings. In these forms, the principal cusps B̲, A̲ and C̲ are more evenly spaced and more similar in height than they are in *Eozostrodon*. The principal cusps of upper and lower molars alternate with one another and the leading edge of the crest joining the individual cusps forms the cutting edge of a series of shearing planes. If the teeth are viewed in the plane of the shearing surfaces (Text-fig. 9, bottom illustration of *Trioracodon*), the cutting edges form a series of V-shaped embrasures (Butler 1972). However, the shearing surfaces of these embrasures differ from the principal shearing surfaces of the molars of therian mammals (see below).

The structure of the principal shearing surfaces of therian mammals is best illustrated in a feline carnassial (Text-fig. 9, *Felis*). Here on the upper PM^4, an inverted V-shaped ridge connects the paracone to the metastylar region. On the matching lower $M_{\bar{1}}$, a V-shaped ridge connects the protoconid and the paraconid. These ridges form the leading or cutting edges of the matching shearing surfaces on the sides of the upper and lower teeth. As these two teeth come into occlusion, the paracone and paraconid meet anteriorly and the metastyle and protoconid meet posteriorly and enclose an ovoid space. As the lower jaw closes, the size of the space progressively diminishes. The advantage of this system is that only two points along opposing cutting edges are closely approximated at any particular moment. These two points move toward the midpoint of the ridge as the jaws close, and the maximum force of the jaws is thus concentrated on a limited area at any given instant in time. The system is therefore ideally suited for slicing through tough food. It has been shown by Dr R. Every (personal communication) and illustrated by Crompton (1971) that the principal shearing surfaces on the anterior and posterior faces of the trigonids and trigons of tribosphenic molars are constructed on the same principle as that operative in the feline carnassial. For purposes of the present discussion, the significant feature of this type of shear is that the matching cusps of upper and lower molars meet point to point at the beginning of shear. This is distinctly different from the triconodontid and eozostrodontid type of shear where the cusps of occluding molars alternate with one another. If the type of occlusion present in *Megazostrodon* were to have been derived from that present in *Eozostrodon*, it would imply a transitional stage in which cusp $\underline{A}$ of the upper (paracone ?) would occlude directly with cusp $\bar{c}$ of the lower (metaconid ?) and cusp $\bar{a}$ of the lower (protoconid ?) with cusp $\underline{B}$ (stylocone ?) of the upper. Mills (1971 : 45) stated : 'It is very difficult to believe that such an arrangement would be advantageous, or even viable, in a shearing dentition. Although less so, it seems unlikely in a non-shearing reptilian dentition' and 'If cusp stood opposite cusp there would be a greater danger of food jamming the jaw'. What Mills is in fact doubting is the structure of the principal shearing surface of the tribosphenic dentition on the posterior surface of the trigonid and the anterior surface of the upper molar (see Text-fig. 11). In order to avoid the problem of having the sides of the tips of cusps occluding directly with one another, Mills suggested that *Eozostrodon* and *Megazostrodon* were both evolved from a form with molar teeth similar to their premolars. He has suggested a series of steps which imply that cusp $\bar{c}$ of *Eozostrodon* is homologous with cusp $\bar{d}$ of *Megazostrodon* and that cusp 'c' of *Megazostrodon* is a new cusp not present in *Eozostrodon*.

It has been shown that in *Megazostrodon* (Text-figs. 6, 9) the principal cusp of the lower molar lies adjacent to or slightly in front of cusp $\underline{B}$ of the uppers and the main cusp of the uppers lies slightly behind cusp $\bar{c}$ of the lowers. Consequently the arrangement of these cusps relative to one another is similar to that of *Kuehneotherium* and more advanced therians. The principal difference is that in *Megazostrodon* the crests joining these cusps lie approximately parallel to, rather than oblique to, the long axis of the jaw, as is the case in *Kuehneotherium*. The leading edges of the ridges joining these cusps in the unworn molars of *Megazostrodon* do not form the cutting edge of the shearing planes as they do in therian molars. The teeth are bulbous and the wear facets are not extensive in the type specimen. Here, as in *Eozostrodon*, wear commences on the cingular area rather than on the sides of the principal cusps.

Characteristic features of undoubted Triassic mammals were a loss of alternate tooth replacement, differentiation of the postcanine row into premolars and molars, cusps to align adjoining molars, and a consistent relationship between upper and lower molars. In *Eozostrodon* the relationship was such that the principal cusp of the lower lay behind cusp B̲. As a result, a wide valley was worn into the upper molar between cusps B̲ and A̲. In *Megazostrodon*, the principal cusp of the lower molar meets the upper molar adjacent to or slightly in front of cusp B̲. Presumably in specimens of *Megazostrodon* showing extensive wear, the front surface of cusp B̲ would be extensively worn. It appears that *Eozostrodon* and *Megazostrodon* are representatives of an early stage of mammalian dental evolution when the positions of the upper and lower molars relative to one another became established in consistent positions. The differences in the relative positions of the molars of *Eozostrodon* and *Megazostrodon* illustrate that the exact position of upper and lower molars relative to one another was not necessarily identical in closely related genera. It has already been shown that in *Thrinaxodon* the relative positions of the postcanines vary in different individuals of the same genus. Because the principal cusps of both upper and lower molars in *Eozostrodon* and *Megazostrodon* occlude initially with the cingular region of the opposing teeth, the morphology of the crown did not play a major role in determining the relative positions. If, on the contrary, this were the case, the differing occlusal patterns in two forms with very similar teeth would not be expected. From what can be determined, the relative positions of upper and lower molars of *Erythrotherium* are the same as those of *Megazostrodon* ; this is despite the fact that the molars of the African *Erythrotherium* are almost identical to those of *Eozostrodon parvus*. This confirms the view that at this early evolutionary stage the occlusal pattern was not determined by the topography of the molar crowns. It is not a question of being obliged to evolve the type of occlusion found in *Megazostrodon* from the type present in *Eozostrodon*, as suggested by Mills (1971), or *vice versa*. It is rather the fixing of the relative positions that is displayed in these two closely related forms. It may not have been very important to these early mammals what the relative positions were, but in terms of evolutionary potential the consequences were far-reaching. From a stage in which the principal cusps of one molar alternated with the subsidiary and principal cusps of the occluding molar, it was possible to evolve the shearing pattern characteristic of the triconodontids ; if, on the other hand, the principal cusps lay adjacent to (or slightly in front of, or slightly behind) intermediary cusps of the occluding molar, it was possible to develop the shearing pattern characteristic of therian molars.

Kuehneotherium is important in this context because its molars show an early stage in the evolution of therian shear. Molar occlusion in *Kuehneotherium* has been discussed by Parrington (1967, 1971, 1973), Crompton (1971) and Butler (1972). The pertinent features are shown in Text-fig. 9. The principal cusp ā of the lower molar (protoconid) occludes directly internal to or slightly in front of cusp B̲ (stylocone) and the principal cusp A̲ of the upper molar (paracone) occludes directly external to or slightly behind cusp c̄ (metaconid) of the lower. After the cingulum of the upper molar located above the region between the stylocone and the paracone has been worn away, two matching shearing planes are formed on the front of the trigon and back of the trigonid. In 1971 (p. 78), I referred to these as shearing plane *1* and have concluded that it is homologous with the shearing plane in the same position on the molars of more advanced therians. Because the tips of the cusps involved come into close contact with one another during occlusion, the trapping ovoid space of therian shearing surfaces was present. However, unlike more advanced therians, this type of shear was not present on the posterior face of the upper molar or the anterior face of the trigonid ; this developed in later forms. It is suggested that in forms directly ancestral to *Kuehneotherium* mammalian type tooth replacement was present, and that cusps forming a 'tongue-in-groove' to align adjoining molars were present. As will be discussed in the next section, the cusps involved were slightly different in *Eozostrodon* and in *Kuehneotherium*. It is also suggested that in the forms ancestral to *Kuehneotherium* the principal cusps were in line and that the principal cusps occluded directly with (or slightly behind or in front of) subsidiary cusps. This arrangement helped to trap the food to be sheared.

There is a problem inherent in having the shearing planes aligned parallel to the long axis of the jaw because tough food would tend to separate the shearing blades, much as the blades of a pair of scissors with a loose hinge can be readily forced apart. This problem can be overcome if the shearing blades are oriented oblique to the long axis of the jaw. It is relatively simple to evolve the *Kuehneotherium* arrangement from that of the hypothetical ancestral stage suggested above, simply by migrating the subsidiary cusp $\bar{c}$ (metaconid) slightly medially (internally) and the subsidiary cusp $\underline{B}$ laterally (externally). Given that cusps forming the shearing planes were arranged to trap the food to be sheared, the efficiency of shearing would be improved if the two subsidiary cusps migrated either internally or externally. Parrington (1971) showed that in a series of *Kuehneotherium* teeth the angles between the metaconid and protoconid in the lowers and paracone and stylocone in the uppers vary considerably. In some specimens they are almost in line, whereas in others they form an angle of nearly 90 degrees. It is interesting to note than in *Kuehneotherium* shearing surfaces of the therian type are present only on the posterior face of the trigonid and anterior face of the trigon. Correlated with this is extensive migration of the stylocone and metaconid. In *Kuehneotherium*, cusp $\underline{C}$[5] of the upper molar and the paraconid do not help to form a therian shearing plane and therefore have not migrated to anything approaching the same extent as the stylocone and the metaconid.

The wear facets of both *Eozostrodon* and *Kuehneotherium* indicate that as the lower jaw closed during mastication, it moved upward and inward during the time when the molar teeth on the active side were in contact. This movement ensures that the chewed food is deposited into the oral cavity rather than remaining between the upper teeth. There is an additional advantage to transverse movements. Kallen & Gans (1972) have determined the contraction sequence of the muscles of mastication in the little brown bat and have concluded that a translatory component during mastication is advantageous as it facilitates tituration and conserves momentum.

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[5] For reasons outlined in an earlier paper (Crompton, 1971) it is doubtful whether cusp $\underline{C}$ is homologous with the therian metacone.

Transverse movements appear to be characteristic of all Triassic mammals and most modern mammals (Mills 1966; Crompton & Hiiemäe 1969; Butler 1972). Transverse jaw movement during occlusion implies that if the lower jaw is viewed from directly in front during mastication, a fixed point on the lower jaw such as the tip of a canine will move in a triangular orbit. As the jaw ramus of the active side opens, it moves directly downward and slightly laterally; it continues to move laterally as it starts to close and it moves medially during the final stage of closing. It was probably as a result of the acquisition of rotary jaw movements in forms ancestral to the Triassic mammals that the external surface of lower postcanines was initially brought into contact with the internal surface of the uppers during the final stage of the masticatory orbit. Bringing the postcanines closer into contact improved the ability to break down food. The loss of alternate tooth replacement, fixing of the relative positions of upper and lower molars, and the alignment of adjoining molars seem to have been features which may well have been selected for after the translatory movement of the jaw was established. There would be little point in selecting for these features unless upper and lower molars were brought into close contact with one another. However, if shearing planes are parallel to the long axis of the jaw, a marked transverse movement during active occlusion would tend to separate the cutting edges. One obvious way to overcome this is to orient the principal shearing planes oblique to the jaw axis. This can be achieved simply by the migration of the subsidiary cusps; *Kuehneotherium* represents an early stage in this development. Having the lower jaw move in a triangular orbit around the longitudinal axis of the jaw requires precise control by the jaw musculature; once this has been achieved, the shearing planes of the occluding teeth can be brought into contact accurately. Without it, the fragile cusps and sharp cutting edges of the teeth could easily be damaged. Precise muscular control of the lower jaw during mastication was independently acquired apparently by mammals and gomphodont cynodonts (plus their descendants, the tritylodonts (Crompton 1972b)). In these forms matching shearing planes were present on the postcanine teeth. A triangular orbit was also established for the lower jaw, but the jaw movements were restricted to a plane parallel to the longitudinal axis of the jaw (i.e. if the skull was viewed from the side rather than the front, the lower jaw would have subscribed a triangular orbit with the lower jaw moving forward during the opening and beginning of the closing phase and backward as the postcanine teeth came into contact. Transverse jaw movements were not possible in gomphodont cynodonts and tritylodonts.

In pantotheres (Text-fig. 9, Dryolestid) and mammals with tribosphenic dentitions, shearing planes designed to trap food to be sheared were established both on the anterior face of the trigonid and the posterior face of the upper molars. The characteristic 'reversed triangles' of therian molars appear to have been initiated because principal and subsidiary cusps occluded directly with one another and, for reasons outlined above, this was followed by rotation of the subsidiary cusps. In triconodonts, the cusps of occluding molars alternated with one another. From such an arrangement, transversely aligned shearing planes could not have evolved by rotation of the cusps, and could only have been achieved by developing an exceptionally wide, bulky tooth incised by two long, deep V-shaped grooves. Rotating cusps and thereby evolving the therian pattern is a simpler and more economical way of achieving obliquely aligned shearing planes.

V. THE RELATIONSHIPS OF *ERYTHROTHERIUM PARRINGTONI*

Mills (1971) pointed out that most features of the molars of *Erythrotherium* can be matched within a large collection of the molars of *Eozostrodon parvus*. He concluded that the differences which I listed in 1964 did not justify placing the southern African form in a separate genus. I agree with his conclusion, but more detailed preparation of the type has subsequently revealed differences which warrant retaining *Erythrotherium* as a separate taxon. Both Mills (1971) and Parrington (1971) stressed that the final upper premolar in *Eozostrodon* is as long as the longest molar and rather higher. This is clearly not the case in *Erythrotherium* where the last upper premolar is smaller than the first molar. There is also no trace of a Kühnecone in the first molar of *Erythrotherium*, but all molars of *Eozostrodon parvus* appear to have a Kühnecone. The relationship between *Erythrotherium* and *Eozostrodon parvus* and *E. oehleri* is, however, extremely close, indicating that the morganucodontids as a group, with many characters held in common, had a wide distribution in late Triassic times, including Europe, China and southern Africa. On the last two continents, early mammals are found together with tritylodontids, and as tritylodontids have been reported from North America (Lewis, Irwin & Wilson 1961) and South America (Bonaparte 1971), it is possible that morganucodontids will eventually be found on these continents as well.

VI. THE RELATIONSHIPS OF *MEGAZOSTRODON RUDNERAE*

In our earlier description (Crompton & Jenkins 1968), *Megazostrodon* and *Eozostrodon* were stated to be closely allied. We followed Parrington (1967) in placing both genera within the Order Triconodonta. In our subsequent paper (Hopson & Crompton 1969), *Megazostrodon, Eozostrodon parvus, E. oehleri, Erythrotherium parringtoni*, and *Sinoconodon rigneyi* were placed in the Family Eozostrodontidae. Hopson (1970) later pointed out that the family name Morganucodontidae had priority. More recently, on the basis of dental occlusion and the relationship between adjacent molars, Mills (1971) placed *Megazostrodon* and *Sinoconodon* in a new family, the Sinoconodontidae. In this section of the paper, *Megazostrodon* will be compared with *Sinoconodon, Eozostrodon, Docodon* and *Kuehneotherium*.

1. *Sinoconodon rigneyi*

Mills (1971) placed particular emphasis on the similarities between the way in which the adjoining lower molars of *Sinoconodon* and *Megazostrodon* contact one another. In *Megazostrodon*, cusp $\bar{d}$ of a lower molar is in line with cusp $\bar{b}$ of the following molar. In the first and second molars of *Megazostrodon* the tip of cusp $\bar{d}$ has been obliterated through wear, but a sufficient area of the crown in this region

Kuehneotheriidae

1. Triangular orbit for active side of jaw.
2. Cusp $\bar{a}$ internal to $\underline{B}$; $\underline{A}$ external to $\bar{c}$ (slight variation).
3. Rotation of cusps to form therian-type shearing surfaces.
4. Mammalian type of tooth replacement.
5. No loss of anterior premolars.
6. Increase in height of cusp $\bar{b}$.
7. Adjoining molars accurately aligned.
8. Cingular cusps absent and development of cingulum on outer surface of lower molars.

Morganucodontidae

1. Triangular orbit for active side of jaw.
2. Cusps and $\underline{A}$ contact opposing cingula in consistent positions in different genera.
3. Cusps in line.
4. Mammalian type of tooth replacement.
5. Loss of anterior premolars.
6. Cusp $\bar{b}$ low.
7. Adjoining molars accurately aligned.
8. Cingulum cusps (external upper and internal lower) well developed.
9. PM5 highly variable.

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Hypothetical Stage A

1. Triangular orbit for active side of jaw.
2. Cusp $\bar{a}$ internal to $\underline{B}$; cusp $\underline{A}$ external to $\bar{c}$ (slight variation).
3. Cusps in line.
4. Mammalian type of tooth replacement.
5. Loss of anterior premolars.
6. Cusp $\bar{b}$ low.
7. Adjoining molars accurately aligned.
8. Cingular cusps reduced in size.

↑ ↑

Hypothetical Stage B

(earliest mammal or cynodont group
from which mammals arose)

1. Triangular orbit for active side of jaw.
2. Cusps $\bar{a}$ and $\underline{A}$ of molars contact opposing cingula, but contact points variable.
3. Cusps in line.
4. Mammalian type of tooth replacement.
5. Loss of anterior premolars.
6. Cusp $\bar{b}$ low.
7. Adjacent molars in close contact.
8. Cusps on internal cingulum of lowers and external cingulum of uppers prominent. Internal cingulum on uppers moderately developed.

↑

Galesauridae

(Early Triassic cynodonts)

1. Jaw movement in vertical plane.
2. No contact between upper and lower postcanines; relative positions variable.
3. Cusps in line.
4. Alternate tooth replacement.
5. Loss of anterior postcanines.
6. Cusp $\bar{b}$ low.
7. Adjoining molars not accurately aligned.
8. Cusps on internal cingulum of lowers prominent. Cingulum and cingular cusps of uppers poorly developed.

is preserved to determine approximately the position of the tip prior to wear. In lateral view, the tip of cusp $\bar{d}$ lies below the tip of cusp $\bar{b}$ of the following tooth (see Text-fig. 6A). The posterior region of the tooth medial to cusp $\bar{d}$ in *Megazostrodon* as seen in crown view is narrow (the 'talonid'). This fits into a shallow concavity on the anterior surface of the following tooth (see M^1 and M^2, Text-fig. 6B) this concavity is flanked medially by the enlarged cusp $\bar{e}$ and laterally by cusp $\bar{b}$. The relationshionship between cusps $\bar{d}$ and $\bar{b}$ is therefore identical in *Eozostrodon* and *Megazostrodon*. In *Eozostrodon*, however, the posterior surface of the molar is wide and only a very shallow concavity exists between $\bar{b}$ and $\bar{e}$. Therefore there is a rather wide, flat contact area between adjoining molars (Text-fig. 3). It should be noted that the more intimate relationship between adjoining lower molars of *Megazostrodon* could quite readily be obtained from the condition in *Eozostrodon* simply by enlarging cusp $\bar{e}$, moving it slightly forward, and narrowing the posterior region of the preceding molar. The junction of two lower molars of *Eozostrodon* is well shown in the stereophotographs in Pl. 3. The arrangement between adjoining teeth in *Sinoconodon* may be similar to that of *Megazostrodon* (unfortunately this area in *Sinoconodon* has not been adequately figured), but as the condition in *Megazostrodon* is so similar to that of *Eozostrodon*, this feature is not a valid reason for placing *Sinoconodon* and *Megazostrodon* in a family which excludes *Eozostrodon*.

Mills (1971) claimed that it is in terms of dental occlusion that the molar teeth of *Megazostrodon* and *Sinoconodon* most closely resemble one another. Unfortunately Mills does not describe the wear facets of *Sinoconodon*. Judging by the loss of all the premolars in the type specimen, it was an old individual and well-defined wear facets would be expected. Mills' conclusions on the relative positions of the upper and lower molars in *Sinoconodon* appear to be based to a large extent upon the spacing of the main cusps. However, as has been shown in the previous section, it is not possible to predict the occlusal relationships between upper and lower molars of morganucodontids from this feature alone.

Although the relative positions of upper and lower molars of *Megazostrodon* and *Sinoconodon* may prove to be identical, there are some striking differences between these two genera. The external cingulum of the uppers and the internal cingulum of the lowers in *Megazostrodon* are enormously developed. Contrast this with the poor development or even total absence of internal and external cingula on the uppers and lowers of *Sinoconodon*. Even the ubiquitous Kühnecone is absent in *Sinoconodon*. In contrast to *Megazostrodon*, in *Sinoconodon* lower molar cusp $\bar{e}$ is widely separated in height from $\bar{b}$. In the type jaw of *Sinoconodon* the last molar was not fully erupted, but all the premolars had already been lost. This is not the case in *Megazostrodon* where the molars are all fully erupted and the premolar loss appears to have commenced only on one side of the lower jaw and to have involved only a single premolar.

It has been suggested (Crompton 1964) that the lower jaw of *Sinoconodon* is similar to that of a galesaurid cynodont and unlike that of *Eozostrodon* or *Megazostrodon*.

FIG. 10. Chart illustrating the stages in the evolution of the principal features of the dentitions of the Morganucodontidae and Kuehneotheriidae.

The individual molars of *Sinoconodon* are almost twice as long as those of *Megazostrodon. Sinoconodon* is not well preserved and, because of these differences and doubt about the dental occlusion, it is suggested that *Megazostrodon* and *Sinoconodon* should not be placed in a family which exludes *Eozostrodon.* The differences between the molars of *Megazostrodon* and *Sinoconodon* are so striking and the similarity between those of *Eozostrodon* and *Megazostrodon* so obvious that there is perhaps a valid reason for placing *Sinoconodon* in a separate family, but until better material has been described, it is convenient to retain *Sinoconodon* in the Morganucodontidae (= Eozostrodontidae).

2. *Eozostrodon parvus* (= *Morganucondon watsoni*) and *E. oehleri*

There are many close similarities between the dentitions of *Eozostrodon* and *Megazostrodon* (compare Text-figs. 3 and 6). For instance, note the relative sizes and positions of the principal cusps, the positions of cingula, the well-developed Kühnecones and the absence of occlusion between the anterior upper and lower premolars. These similarities, in addition to the structures of the skull and skeleton (to be described in later papers), appear to indicate a close relationship between the two genera. The differences in molar structure of *Megazostrodon* and *Eozostrodon* are in part differences in the relative size of cusps and cingula. For example, in *Megazostrodon* the cingula and cingular cusps, cusp ē and the Kühnecone are considerably larger than in *Eozostrodon.*

A fairly marked distinction between *Megazostrodon* and *Eozostrodon* is that in the former the last upper premolars are not larger than the first molar ; the reverse is true for *Eozostrodon.* The other major difference stressed by Mills (1971) is in the patterns of molar occlusion. This has been discussed in the previous section. In $M_{\bar{2}}$ of *Megazostrodon,* a cingulum is present antero-medial to cusp ē and a cingulum is present internal to the Kühnecone in $M_{\bar{3}}$. The cusps of the buccal cingulum of the upper molars of *Megazostrodon* are large and the internal surface is convex ; as a result the tooth in crown view is kidney- or bean-shaped. The lingual cingulum of the upper molars is less cuspidate than in *Eozostrodon.* The posterior part (the 'talonid') of the lower molars is relatively longer and narrower in *Megazostrodon* than in *Eozostrodon.* Premolar loss in *Megazostrodon* appears to commence only after the complete eruption of $M_{\bar{4}}$, and there is no marked decrease in size of the lower molars going in a posterior direction ; this is a feature characteristic of many of the lower jaws of *Eozostrodon.*

The extensive loss of anterior postcanines in some individuals of *Eozostrodon* and eruption of a small, apparently non-functional terminal lower molar in *Eozostrodon* are reminiscent of the conditions in cynodonts such as *Thrinaxodon* (Crompton 1963). If premolar loss in *Megazostrodon* was less extensive than in *Eozostrodon,* this could be interpreted as an advanced feature.

The similarities and differences of the molar and occlusal patterns of *Eozostrodon* and *Megazostrodon* suggest that the common ancestor of these genera (Hypothetical Stage B, Text-fig. 10) had molar teeth and a tooth replacement pattern similar to those of *Eozostrodon.* In this common ancestor, during mastication the molars of the active side would have been beginning to contact the cingular areas of opposing molars. There was probably a significant amount of variation in the relative positions of upper and lower postcanines, but because the upper and lower unworn molars did not have matching shearing planes, the exact position of the initial contact in a young animal was not important. In *Eozostrodon*, the contact point of the cusp ā of the lower molar was established behind cusp B̲ of the upper ; in *Megazostrodon*, the contact point was in front of cusp B̲. In addition, in this form the external and internal cingular cusps of the upper and lower molars respectively increase in size, the contact point between adjacent lower molars was modified in a slightly different way from that of *Eozostrodon* and the posterior premolars were not enlarged. Some of the lower postcanines of the Morganucodontidae are very similar to those of *Thrinaxodon*, and if it is accepted that the Galesauridae (= Thrinaxodontidae) included the ancestors of the Morganucodontidae, the main steps that seem to have taken place in evolving the postcanine dentition of the latter from the former are :

(1) Establishing a triangular masticatory orbit for the active side of the lower jaw (see p. 422) so that the postcanine teeth were brought into contact during mastication. Initially it was presumably only the posterior postcanines which came into contact. This is inferred because in the Morganucodontidae the anterior premolars still did not contact one another during mastication.

(2) Developing a mammalian type of tooth replacement in which the milk molars are replaced once by premolars and molars which were not replaced added sequentially from front to back. The steps involved in the transition have been discussed by Osborn and Crompton (1972). *Thrinaxodon* is characterized by loss of several of the anterior postcanine teeth, and this feature is also characteristic of the Morganucodontidae.

(3) Establishing a fixed relationship between the upper and lower molars and developing small cusps to align adjoining molars. This was achieved in slightly different ways in *Eozostrodon* and *Megazostrodon*.

3. *Docodon*

It is generally accepted that lower molars of *Eozostrodon* are similar to those of *Docodon* and that it is possible to derive the latter from the former. However, the upper molars of *Docodon* differ from those of *Eozostrodon* in possessing a well-developed internal cusp which bites into the basin formed between two adjacent lower molars. Crompton and Jenkins (1968) attempted to show how the transition from *Eozostrodon*-type upper molars to *Docodon*-type upper molars could have taken place. Several aspects of the dentition of *Megazostrodon* are reminiscent of *Docodon* (Jenkins 1969). For example, the antero-internal cusp ē of the lowers of *Megazostrodon* is enlarged, making the anterior region of the crown relatively wider than it is in *Eozostrodon* (see Crompton & Jenkins 1968, fig. 7). A cingulum is present anterior to cusp ē in *Megazostrodon* and a similar feature is present in *Docodon*. In *Docodon* the Kühnecone is larger than in any of the morganucodontids and of these it is largest in *Megazostrodon*. In M_3 of *Megazostrodon* cusp c̄ is considerably reduced in size and in *Docodon* it is absent. It has been suggested (Crompton & Jenkins 1968) that the development of the medial cusp of the upper molars of *Docodon* was in part related to a decrease in size and ultimate disappearance of cusp c̄.

However, the enlarged external cingulum of the upper molars of *Megazostrodon* is not found in *Docodon* where this feature is poorly developed. This evidence suggests that *Docodon* was probably derived from an as-yet-unknown eozostrodontid rather than specifically from *Eozostrodon* or *Megazostrodon*.

4. *Kuehneotherium praecursoris*

Mills (1971) stated that there is a fundamental difference between the molars of *Kuehneotherium* and *Eozostrodon*. In *Kuehneotherium* (Text-fig. 7), the principal cusps form a triangle, obtuse in the anterior molars and more acute in the posterior (Parrington 1967, 1971, 1973); cusps $\bar{b}$ and $\bar{c}$ are high and distinct from the cingulum. In *Eozostrodon*, on the other hand, $\bar{b}$ is low and has been termed a cingular cusp by Mills. In *Kuehneotherium*, the internal cingula of the uppers are narrow and non-cuspidate, whereas they are cuspidate in *Eozostrodon*. There is a weak external cingulum in the lowers of *Kuehneotherium*; in *Eozostrodon* it is at most present in the form of an occasional cuspule (Parrington 1971). The strongly cuspidate internal cingulum of the lowers of *Eozostrodon* is absent in *Kuehneotherium*. In *Kuehneotherium* a small 'talonid' heel supporting cusp $\bar{d}$ is present. It projects between cusps $\bar{e}$ and $\bar{f}$ on the anterior surface of the succeeding molar. In *Eozostrodon*, a distinct 'talonid' heel is absent but the broad posterior region of the molar fits into a shallow embayment between cusps $\bar{b}$ and $\bar{e}$ on the succeeding molar. The other difference between *Eozostrodon* and *Kuehneotherium* is the relative position of the upper and lower molars (discussed on p. 420).

Although the molars of *Megazostrodon* are similar to those of *Eozostrodon*, the former possess some of the features which characterize *Kuehneotherium*. For example, the relative positions of upper and lower molars is the same, the internal cingulum of the uppers of both *Megazostrodon* and *Kuehneotherium* is poorly developed, and the three main cusps of M^1 and M^2 of *Megazostrodon*, rather than being in line, form an obtuse triangle. In these two molars in *Megazostrodon* the external surface of the crown is concave and the internal surface convex; this is also true of *Kuehneotherium* molars. In $M_{\bar{1}}$ and $M_{\bar{2}}$ of *Megazostrodon* a 'talonid' is present and fits into a shallow embayment on the anterior surface of the succeeding tooth. This lies between cusp $\bar{e}$ and cusp $\bar{b}$ in *Megazostrodon*, whereas in *Kuehneotherium* it lies between cusps $\bar{e}$ and $\bar{f}$. This difference may be related to the more medial position of cusp $\bar{b}$ in *Kuehneotherium*; in this case cusp $\bar{f}$ would have developed to form an outer wall to the embayment. Cusp $\bar{b}$ becomes separate from cusp $\bar{a}$ at a higher level in *Kuehneotherium* than in *Eozostrodon*. In *Kuehneotherium*, cusp $\bar{b}$ is widely separated from cusps $\bar{e}$ and $\bar{f}$; in *Megazostrodon*, on the other hand, cusp $\bar{e}$ is large and lies slightly in front of cusp $\bar{b}$ so that cusp $\bar{b}$ appears to be more of a crown cusp than a cingular cusp. Mills draws a sharp distinction between cingular and crown cusps, and on this basis has claimed that cusps $\bar{b}$ of *Kuehneotherium* and of *Eozostrodon* are not homologous. However, it has been shown in *Megazostrodon* that clearly homologous cusps may appear in one molar of a postcanine row as a cingular cusp and in another as a crown cusp. Except for the strong external cingulum, upper M^1 of *Megazostrodon* bears a striking resemblance to Sy_7 of Parrington (1971, fig. 13). The actual advanced feature of *Kuehneotherium* molars is that less of the tooth has to be worn away to produce the wear facets on the posterior surface of the trigonid and anterior face of the trigon. In addition, this facet is oblique to the longitudinal axis of the jaw.

Mills (1971) stressed the differences in morphology of the molar roots of *Eozostrodon* and *Kuehneotherium*. Although *Megazostrodon* is a mature individual, there are no indications of expansion of the root tips. This problem has been fully discussed by Parrington (1973). In *Kuehneotherium* there is no evidence of the loss of anterior premolars with increasing maturity. In the single specimen of *Megazostrodon*, only one of the premolars appears to have been lost.

Given the range of variation of the molar patterns of the Morganucodontidae, the most significant differences between the known members of this family and the Kuehneotheriidae appear to be : (1) the way in which the adjoining lower molars meet one another and (2) the rotation of some of the subsidiary cusps to form shearing planes oriented obliquely to the longitudinal axis of the jaw.

In Text-fig. 10, the steps in evolving the dentitions of these two families of Triassic mammals from a form of galesaurid such as *Thrinaxodon* are summarized. Two hypothetical intermediate stages have been postulated in the evolution of the dentition of *Kuehneotherium*. In Hypothetical Stage B (ancestral to both the Morganucodontidae and Kuehneotheriidae) the common features of both families are present, including a triangular masticatory orbit, postcanine teeth beginning to contact one another during mastication, mammalian type of tooth replacement and close contact between adjoining molars.

In forms where the postcanine teeth contact one another and where a fixed relationship has been established between upper and lower teeth, the advantage of accurately aligning adjoining molars is that it helps position the teeth accurately as they erupt (Hopson, personal communication). As molar occlusion became more effective in the lines leading to the eozostrodontids and kuehneotheriids, the way in which the molars were aligned developed slightly differently in each. In the line leading to morganucodontids, this was formed by the posterior part of one molar fitting into a shallow embayment between cusp ē and cusp b̄ ; in the latter line by cusp d̄ fitting into an embayment between cusp ē and a new cusp, f̄. The presence of this latter feature, a reduction of the size of the cingular cusps and a fixing of the relative positions of upper and lower molars would have been characteristic features of a Hypothetical Stage A form. The Kuehneotheriidae could have evolved from this stage by rotating the cusps (see discussion on molar occlusion, p. 415), retaining the anterior premolars for a longer portion of the life span, increasing the height of cusp b̄ and reducing the cingular cusps further.

If this analysis is correct, it would suggest that both the Kuehneotheriidae and the Morganucodontidae could have been derived from an advanced galesaurid cynodont in which a triangular masticatory orbit had been established. The middle Triassic cynodont *Probainognathus* (Romer 1969, 1970 ; Crompton 1972a) appears to be closely related to the phylogenetic line between a galesaurid and Hypothetical Stage B. In *Probainognathus*, the dentary forms part of the articulation with the squamosal, the postcanine teeth appear to have contacted one another during mastication, and the tooth replacement pattern is more mammalian than in

Thrinaxodon (J. Osborn, personal communication). *Probainognathus* does not appear to have been on the direct phylogenetic line leading to the Kuehneotheriidae and Morganucodontidae because the cingular cusps, although present, are less well developed than in *Thrinaxodon*.

5. Amphilestinae

Mills (1971) pointed out the strong similarity between the teeth of the Amphilestinae and *Kuehneotherium* ; he suggested that these forms be removed from the Triconodontidae. Mills noted that in the Amphilestinae the principal upper molar cusp $\underline{A}$ sheared either against cusp $\bar{d}$ or cusp $\bar{b}$ of the succeeding lower molar. Judging from stereophotographs of a left ramus of *Amphilestes broderipii* in the University Museum at Oxford, the principal cusp of the upper molar occluded between cusps $\bar{f}$ and $\bar{b}$ and in this respect they resemble the late Jurassic symmetrodont *Tinodon* (Crompton & Jenkins 1968) more than *Kuehneotherium*. If a close relationship between the amphilestines, *Kuehneotherium*, and the late symetrodonts is confirmed, it will support the view that the triangular arrangement of the principal cusps in therians was derived from a form in which these cusps were more nearly in a straight line. It may, therefore, have been possible to derive the Amphilestinae from Hypothetical Stage A (Text-fig. 10). It is interesting to note that in this family both cusps $\bar{e}$ and $\bar{f}$ are present and that the way in which lower molars contact one another is probably the same as in *Kuehneotherium*.

6. Haramiyidae

The isolated teeth of the Haramiyidae (Parrington 1946) remain an enigma, but on the basis of the morphology of the posterior premolars and anterior molars of the Guimarota multituberculate, Hahn (1969) suggested that the haramiyid teeth may have been present in an early mammal which was related to, or ancestral to, the multituberculates. If this comparison is valid, it may be possible to determine the position of some of the haramiyid molars. For example, the teeth assigned to *Microcleptes moorei* (Simpson 1928) may be upper postcanines. In this case, the row of three cusps would be homologous to the principal cusps of the morganucodontids (cusps $\underline{B}$, $\underline{A}$ and $\underline{C}$), and the outer cusp row consisting of a high anterior cusp followed by a series of smaller cusps would be homologous to the cingular cusps of morganucodontids. *Megazostrodon* is characterized by a well-developed external cingulum on the upper molars ; on M^2, M^3 and M^4 the anterior cingular cusp is the largest of the cingular cusps. This is extremely slender evidence upon which to base a haramiyid–morganucodontid relationship, and at the most suggests that the haramiyid molars could have been derived from a form ancestral to the Morganucondontidae by enlargement and modification of the cingular cusps.

The wear patterns of haramiyid teeth have not been studied in detail, but some of the heavily worn specimens suggest a triangular masticatory orbit having a power stroke with a transverse component. If this is true, it would mean that the anterior to posterior (or posterior to anterior) power stroke of the multituberculates must have been a secondary specialization in this group, much the same as it subsequently was in some rodents. The basic pattern of mammalian jaw musculature having been established, it would have been relatively simple for rodents to shift the direction of the power stroke because the lower jaw is held suspended in a sling of musculature (Hiiemäe 1971).

VII. CONCLUSIONS

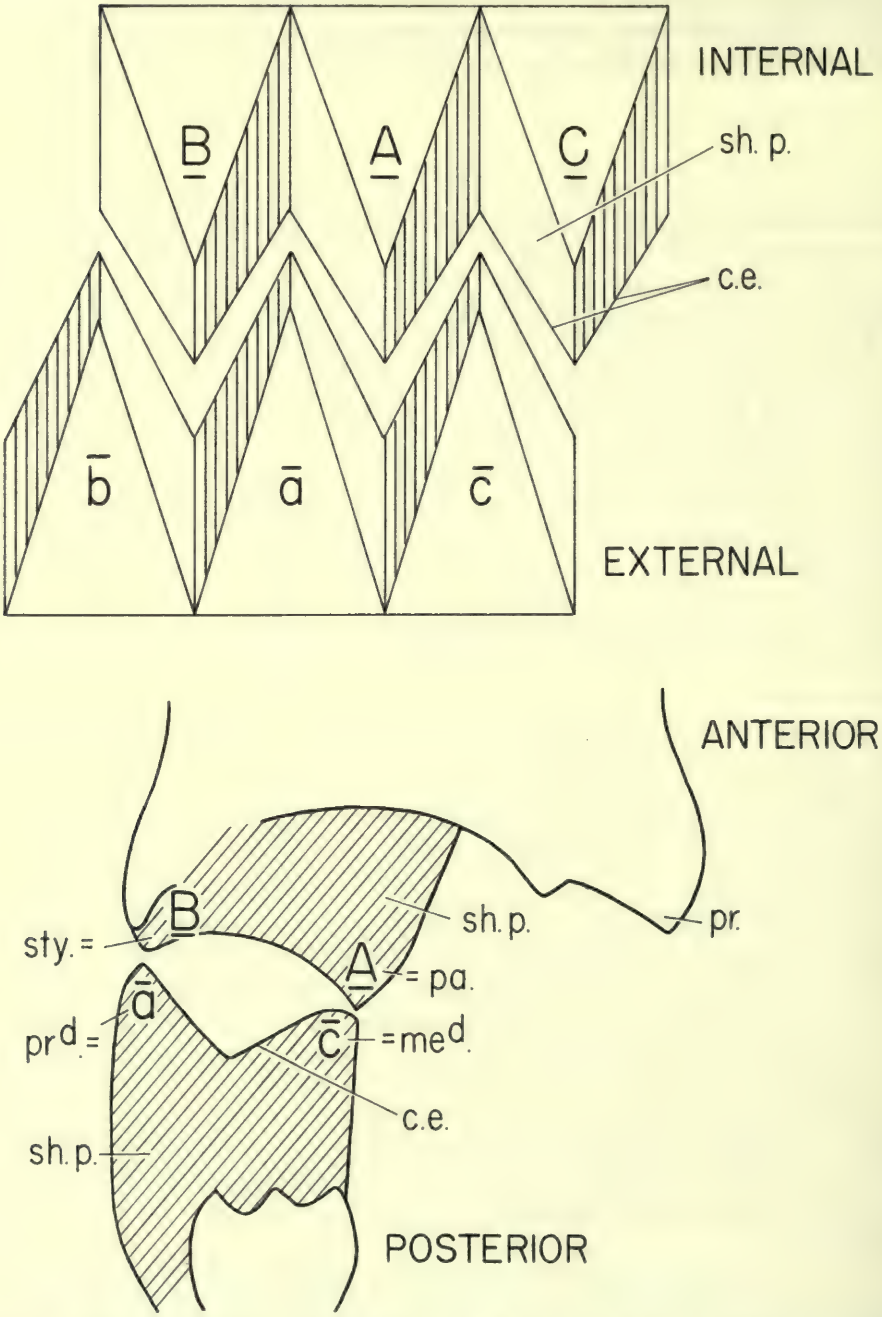
A detailed study of the dentitions of *Erythrotherium parringtoni* and *Megazostrodon rudnerae* has shown that these forms are closely related to *Eozostrodon* (= *Morganucodon*) *parvus* and *E. oehleri* and that they should all be included in the Family Morganucodontidae (= Eozostrodontidae). *Sinoconodon rigneyi* is poorly known and it is suggested that it should also perhaps be included in this family. It is concluded that there is no convincing reason supporting Mills' (1971) suggestion that *Sinoconodon* and *Megazostrodon* be placed in a separate family, the *Sinoconodontidae*, in which *Eozostrodon* and *Erythrotherium* are not included. If this family is to be retained, it should include only *Sinoconodon* and certainly not *Megazostrodon*.

The principal differences between the dentitions of the different genera included in the Morganucodontidae are the degree of development of the cingular cusps of the molars, the relative sizes of the last premolars, and the positions of upper and lower molars relative to one another.

A study of molar occlusion in the triconodonts has confirmed the generally accepted view that this group could have been derived from morganucodontids in which the relative positions of upper and lower molars were similar to that in *Eozostrodon*, rather than that in *Megazostrodon* and *Erythrotherium*. It is tentatively suggested that the molars of the haramiyids could possibly have been derived from a form immediately ancestral to the Morganucodontidae.

It has been concluded that the dentitions of the Morganucodontidae and of the Kuehneotheriidae are sufficiently alike to suggest a fairly close relationship. The principal differences are the way in which adjoining lower molars contact one another, a rotation of the subsidiary cusps in the latter family, and the presence on each molar of at least one major therian-type shearing surface which is aligned oblique to the long axis of the jaw in the Kuehneotheriidae. The dentitions of both families could have been derived from an advanced galesaurid (= thrinaxodontid). The way in which the lower molars of *Amphilestes* meet one another confirms the view that these forms are more closely related to *Kuehneotherium* than to the Morganucodontidae. *Amphilestes* appears to have arisen from the same group that gave rise to keuhneotheriids. The cusps of the amphilestines are in line, and this supports the view that the triangular arrangement of the cusps of *Kuehneotherium* arose by rotation of the subsidiary cusps rather than by the development of new cusps on the flanks of the principal cusps.

On the basis of wear surfaces on the molars, it is confirmed that in all the Triassic mammals, only one side of the jaw was actively involved in mastication at any one time and that during the final stages of jaw closure the jaw moved not only vertically but slightly medially as well. Consequently, if the active lower jaw were viewed from directly in front, during mastication the long axis of the jaw (and naturally


INTERNAL
B
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prd. =
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= med.
c.e.
sh. p.
POSTERIOR

FIG. 11. Comparison of the principal shearing surfaces in the molars of triconodonts and therian mammals. See the text for explanation.

also the individual teeth) would move in a triangular orbit. As the jaw opened and started to close, it moved laterally and as the teeth approached one another until the jaw was fully closed, it moved vertically and medially. It appears that in the Galesauridae (= Thrinaxodontidae), which appear to have been ancestral to the Triassic mammals, the opening and closing jaw movements were restricted to the vertical plane ; the sides of the postcanine teeth were not brought into close contact during the final stages of mastication and food was possibly broken up by both sides of the jaw simultaneously. (This latter feature is also characteristic of gomphodont cynodonts.) Therefore, matching shearing surfaces are not found on the postcanines of the Galesauridae. With the introduction of a triangular orbit for the lower jaw, the lower postcanines were brought into closer contact during the chewing cycle. This must have improved the ability of these teeth to break down food. Their efficiency would have been further increased if they developed accurately matching shearing planes on upper and lower postcanines. This required two important changes : (1) fixing the positions of upper and lower postcanines relative to one another and (2) modification of the alternate tooth replacement pattern to one in which the molars are added in both upper and lower jaws sequentially from front to back. In therians, shearing surfaces on a single molar are matched by those on two molars of the opposite jaw. Alternate replacement would disrupt these shearing planes. Once these changes had been incorporated into the dentitions, it was possible to develop consistent, accurately matching shearing surfaces on individual postcanine teeth. The position and morphology of these shearing surfaces in later mammals were initially determined by the relative positions of upper and lower postcanines in the earliest mammals. In the Jurassic triconodonts, the cusps of the upper and lower molars alternated with one another resulting in cusps of one molar shearing down V-shaped grooves between the cusps on the occluding molar and *vice versa* (see Text-fig. 11A). This appears to have developed from the pattern in Triassic mammals such as *Eozostrodon* where the principal cusp of the lower molar initially contacted the cingulum of the upper postcanine external to the gap between its principal cusp $\underline{A}$ and its anterior subsidiary cusp $\underline{B}$.

In therian mammals, the principal shearing surfaces (Text-fig. 11B) are not present on the sides of the V-shaped grooves between the main cusps. Rather, a single shearing surface lies above or below two cusps and the ridge joining the tips of the two cusps forms the leading or cutting edge of a single shearing surface. Consequently, the sides of the tips of the cusps involved meet one another, rather than alternating. In the therian type of shearing, the food to be sheared is trapped in the ovoid space between the four cusps involved. This type of shear appears to have evolved from Triassic mammals in which the principal cusp of the upper molar initially contacted the cingulum of the lower molar directly external to or slightly behind the posterior subsidiary cusp of the lower, cusp $\bar{c}$, and the principal cusp of the lower molar contacted the cingular area of the upper directly internal to or slightly in front of the anterior subsidiary cusp $\underline{B}$ of the upper molar. The rotation of the cusps in therians appears to be an adaptation to keeping the principal shearing surfaces in contact as the transverse component of the masticatory orbit increased in magnitude.

In *Amphilestes*, the relative position of upper and lower molars is slightly different from that of the kuehneotheriids. This confirms the view that this was a highly variable feature in early mammals, and that in the different phyletic lines different positions were selected for.

As is well known, the cynodonts are all characterized by a progressive increase in the size of the dentary and relative increase in the mass of jaw musculature. As a result, in advanced cynodonts the jaw joint, despite the surangular–squamosal contact, tended to be relatively less substantial than in the earlier therapsids. In order to reduce the forces acting through the jaw joint, the jaw muscles evolved so as to increase the power of the bite across the postcanine teeth without placing undue strain on the jaw articulation. An important advantage of this type of arrangement of jaw musculature was increased control and mobility of the lower jaw, permitting not only vertical opening and closing movements, coupled with varying degrees of antero-posterior movement, but also permitting transverse movement of the jaw to take place. A result of this was that the longitudinal axis of the lower jaw could follow a triangular orbit during mastication. Consequently, the sides of the upper and lower postcanines on one side could be brought into closer contact than was possible in the earlier carnivorous cynodonts. In addition, the jaw movements could be sufficiently controlled so that occluding teeth were not damaged by malocclusion. The other mammalian features of the masticatory apparatus, the tooth replacement pattern and consistent and accurately matching shearing planes on occluding molars could only develop once the increased mobility, but more important, the precise control of the lower jaw had evolved. This control appears to have been a spin-off from offloading of the jaw joint. In cynodonts and mammals it was probably only when the bite was across the postcanine teeth that the vertical forces acting through the jaw joint could be reduced because of the arrangement of the muscles. If the front of the jaw was used, the jaw joint would have been load bearing (Hiiemäe 1971). It may be possible to correlate the rapid evolution in size and complexity of the postcanine teeth in these groups with this feature. The more primitive therapsids, the therocephalians and gorgonopsids, are characterized by powerful incisors and canines and rather weak postcanines. The reverse is true of the Triassic mammals and advanced cynodonts.

The gomphodont cynodonts and tritylodontids which also substantially reduced the size of the jaw articulation had to meet the problem of reducing the forces across the jaw joint at the same time as they increased the power of bite across the postcanines. The jaw muscle arrangement which evolved in these groups also permitted a greater mobility and control of the lower jaw. Matching shearing planes developed on upper and lower postcanine teeth and the reptilian tooth replacement pattern was modified to one in which teeth which had accurately matching shearing surfaces were added sequentially at the posterior end of the row. In addition, the postcanine row was not disrupted by alternate tooth replacement. However, in these forms jaw movements were vertical or parallel to the postcanine tooth rows ; transverse jaw movements were not possible. The only therapsid group which substantially reduced the size of the reptilian jaw joint and which also developed a squamoso-dentary articulation were the ictidosaurs. These retained alternate tooth replacement of the postcanines and transverse jaw movements were apparently not possible.

The transverse jaw movements, together with the limiting of tooth replacement to deciduous and permanent teeth, the division of the postcanine row into premolars and molars and the fixing of the relative positions of upper and lower molars are characteristic features of all the known Triassic mammals. These features clearly separate Triassic mammals from all known therapsids. It is concluded that this mosaic of features arose in an advanced galesaurid cynodont that lived during middle Triassic time. As far as can be determined at the present time, it is only in the advanced cynodonts that the reptilian jaw musculature underwent the changes which are essential for the evolution of a mammalian type of masticatory apparatus. For this reason it is doubtful whether mammals could be derived from any group other than the cynodonts.

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A. W. Crompton
Department of Biology and Museum of Comparative Zoology
Harvard University
Cambridge
Massachusetts
U.S.A.

PLATE 1

Premolars and molars of *Erythrotherium parringtoni* and *Megazostrodon rudnerae*. All × 35.

A. *Erythrotherium parringtoni*, external view of upper R. M^2.
B. *Erythrotherium parringtoni*, crown view of upper R. M^2.
C. *Megazostrodon rudnerae*, internal view of lower R. $PM_{\bar{5}}$.
D. *Megazostrodon rudnerae*, internal view of lower L. $M_{\bar{1}}$.
E. *Megazostrodon rudnerae*, internal view of lower R. $M_{\bar{2}}$.
F. *Megazostrodon rudnerae*, internal view of lower R. $M_{\bar{3}}$.

PLATE 1

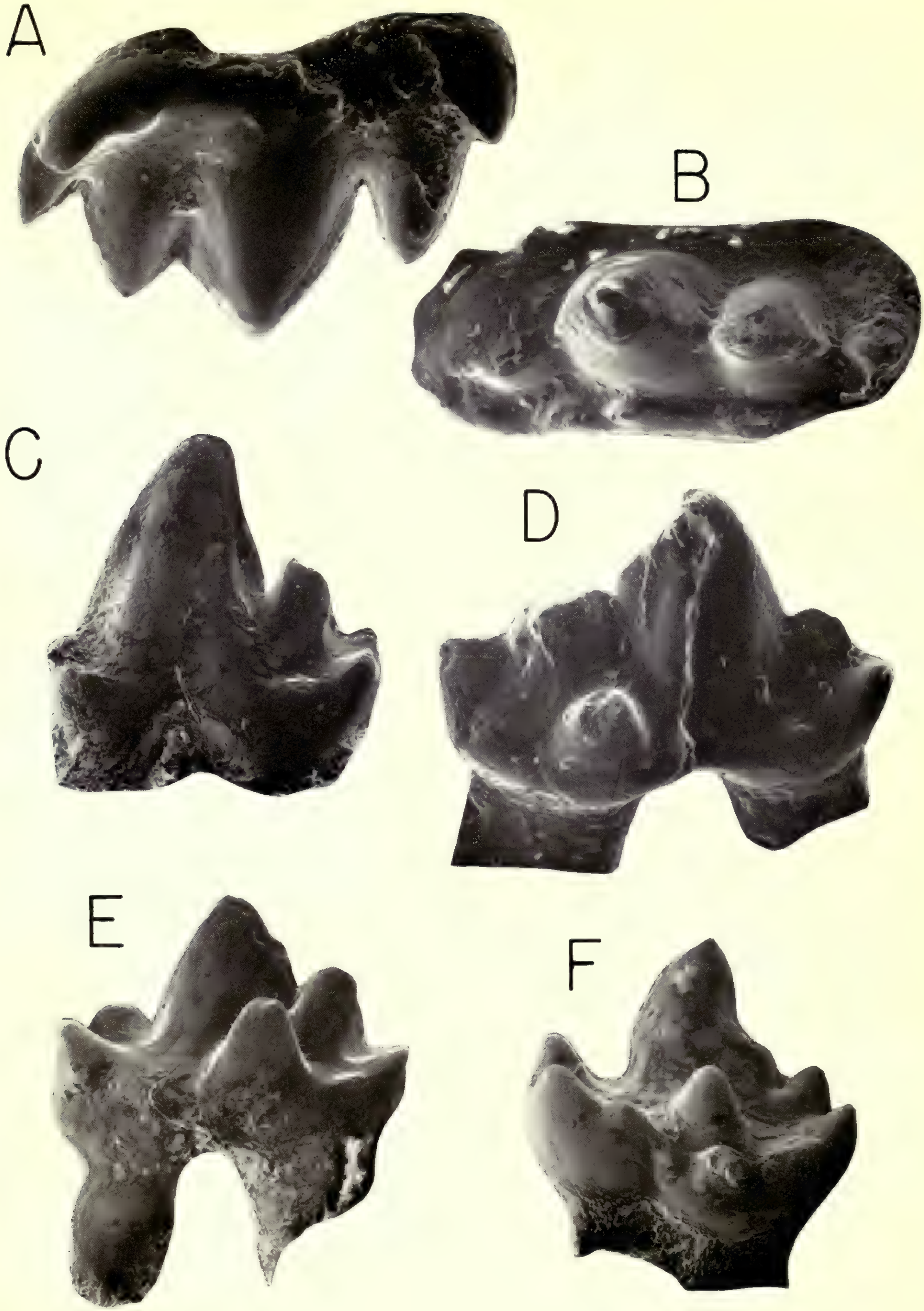


PLATE 2

Upper premolars and molars of *Megazostrodon rudnerae*. All × 35.

A. External view of R. $\mathrm{PM}^{\underline{5}}$.
B. External view of R. $\mathrm{M}^{\underline{1}}$.
C. Internal view of L. $\mathrm{M}^{\underline{1}}$.
D. External view of R. $\mathrm{M}^{\underline{2}}$.
E. External view of R. $\mathrm{M}^{\underline{3}}$.
F. External view of R. $\mathrm{M}^{\underline{4}}$.

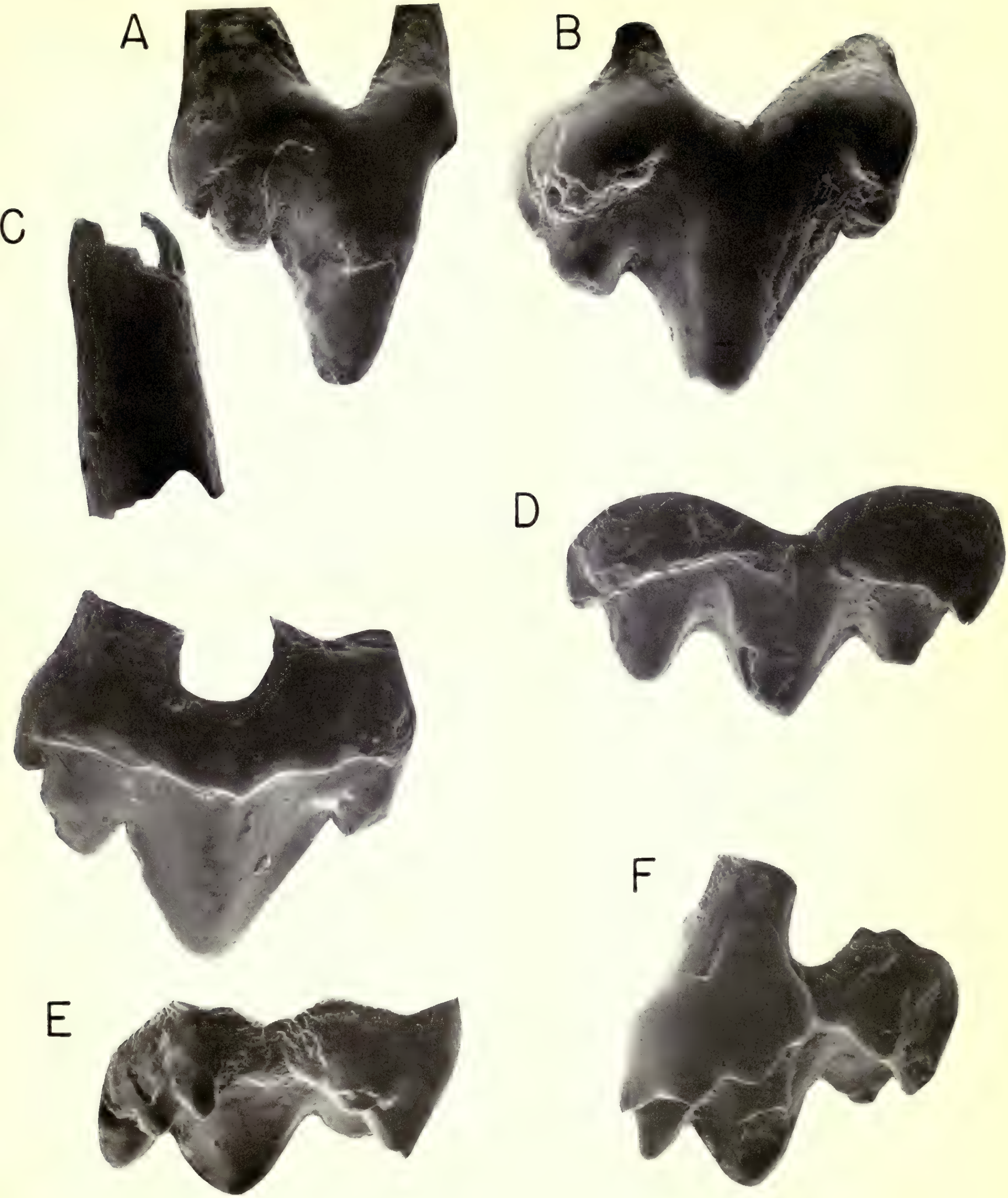

A
B
C
D
E
F

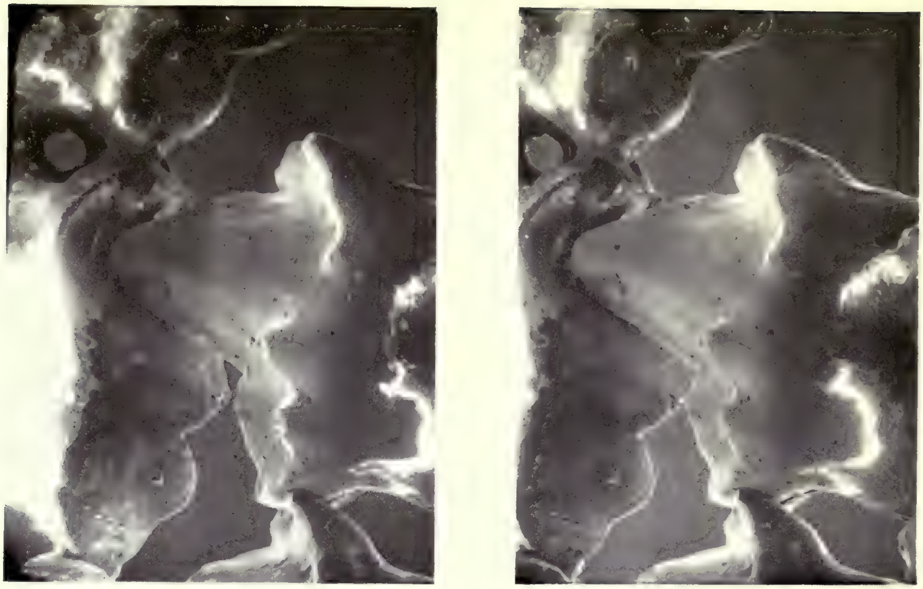
PLATE 3

Stereophotographs of occlusal details of molars of *Eozostrodon parvus*.

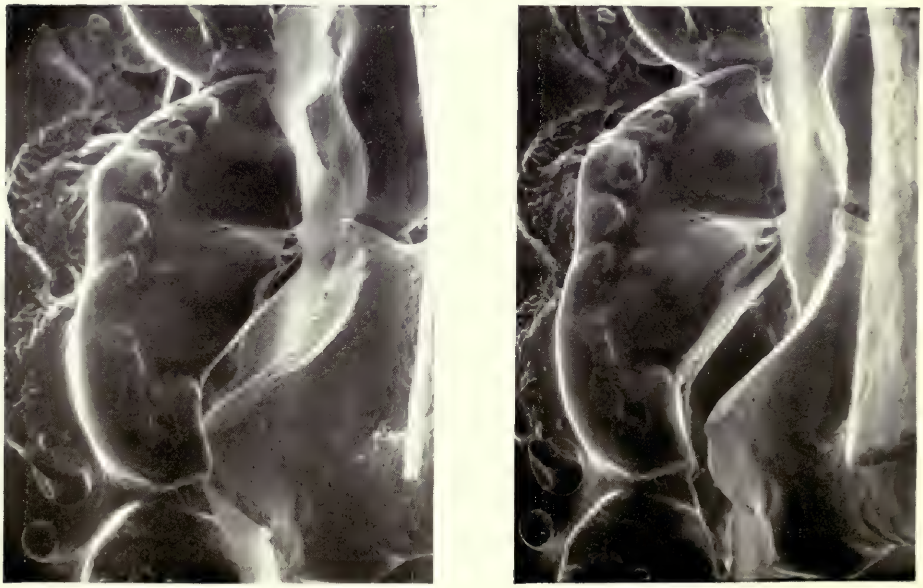
A. Internal view, × 39.

B. Oblique external view, × 41.

A



B



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